# THE DESIGN AND ANALYSIS OF SALMONID TAGGING STUDIES IN THE COLUMBIA BASIN

### **VOLUME XVII**

Effects of Ocean Covariates and Release Timing on First Ocean-Year Survival of Fall Chinook Salmon from Oregon and Washington Coastal Hatcheries

Prepared by:

Caitlin Burgess John R. Skalski

Columbia Basin Research University of Washington 1325 Fourth Avenue, Suite 1820 Seattle, Washington 98101-2509

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U.S. Department of Energy Bonneville Power Administration Environment, Fish and Wildlife P.O. Box 3621 Portland, OR 97208-3621

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#### Other Publications in this Series

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- **Volume VIII:** Lowther, A. B., and J. R. Skalski. 1998. Improved survival and residualization estimates for fall chinook using release-recapture methods. Technical Report (DOE/BP-02341-6) to BPA, Project 89-107-00, Contract 90-BI-02341.
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- **Volume X:** Westhagen, P., and J. R. Skalski. 1998. Instructional guide to using program CaptHist to create SURPH files for survival analysis using PTAGIS data files. Technical Report

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(DOE/BP-02341-4) to BPA, Project 89-107-00, Contract 90-BI-02341.

- **Volume XI:** Skalski, J.R., R.L. Townsend, A.E. Giorgi, and J.R. Stevenson. Submitted. Recommendations on the design and analysis of radiotelemetry studies of salmonid smolts to estimate survival and passage efficiencies. Technical Report to BPA, Project 89-107-00, Contract DE-BI79-90BP02341. 33 pp.
- **Volume XII:** Ryding, K.E., and J.R. Skalski. 1999. A multinomial model for estimating ocean survival from salmonid coded wire-tag data. Technical Report (DOE/BP-91572-3) to BPA, Project 91-051-00, Contract 96-BI-91572.
- **Volume XIII:** Perez-Comas, J.A. and J.R. Skalski. 2000. Appraisal of system-wide survival estimation of snake river yearling chinook salmon using pit-tags recovered from caspian tern and double-crested cormorant breeding colonies on Rice Island. Technical Report to BPA, Project No. 8910700, Contract DE-BI79-90BP02341.
- **Volume XIV:** Perez-Comas, J.A. and J.R. Skalski. 2000. Appraisal of the relationship between tag detection efficiency at Bonneville Dam and the precision in esuarine and marine survival estimates of returning pit-tagged chinook salmon. Technical Report to BPA, Project No. 8910700, Contract DE-BI79-90BP02341.
- **Volume XV:** Perez-Comas, J.A. and J.R. Skalski. 2000. Appraisal of the relationship between tag detection efficiency at Bonneville Dam and the precision in-river survival estimates of returning pit-tagged chinook salmon. Technical Report to BPA, Project No. 8910700, Contract DE-BI79-90BP02341.
- **Volume XVI:** Skalski, J.R and J.A. Perez-Comas. 2000. Alternative Designs for Future Adult PIT-tag Detection Studies. Technical Report to BPA, Project No. 8910700, Contract DE-BI79-90BP02341.

#### Other Publications Related to this Series

Other related publications, reports and papers available through the professional literature or from the Bonneville Power Administration (BPA) Public Information Center - CKPS-1, P.O. Box 3621, Portland, OR 97208.

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## **Preface**

Project 91-051 was initiated in 1991 in response to the Endangered Species Act (ESA) listings in the Snake River Basin of the Columbia River Basin. One of the primary objectives of this project was to address the need for further synthesis of historical tagging and other biological information to improve understanding and identify future research and analysis needs. This report is one in a series illustrating statistical methods for performing Pacific Northwest salmon tagging studies. The goal of this series is to present state-of-the-art statistical methods that can more properly and more efficiently extract information from historical tag data, and to provide quantitative guidance on the design and analysis of tagging studies to investigators interested in generating reliable information for the management of salmonid resources in the Northwest.

This study is a followup to Volume XII of this series which applied multivariate analysis to age-at-return data on coho salmon reared in coastal hatcheries in Washington state and implanted with coded wire tags (CWTs). This followup analyzes CWT release and recovery data on fall chinook salmon from coastal hatcheries in Oregon and Washington state. The specific objective of both studies was to understand relationships between survival and ocean conditions during the first year in marine habitat, a period believed to be a primary determiner of cohort strength. The archive of CWT data, still largely unmined, makes possible investigations into thirty years of oceanographic effects on salmonid survival. The intent of these studies is to supply timely and crucial information linking first ocean-year conditions to salmonid survival in order to inform harvest, supplementation and other policies which have as their goal the recovered and/or continued viability of ecologically significant units in the Pacific Northwest.

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#### **ABSTRACT**

Effects of oceanographic conditions, as well as effects of release-timing and release-size, on first ocean-year survival of subyearling fall chinook salmon were investigated by analyzing CWT release and recovery data from Oregon and Washington coastal hatcheries. Age-class strength was estimated using a multinomial probability likelihood which estimated first-year survival as a proportional hazards regression against ocean and release covariates. Weight-at-release and release-month were found to significantly effect first year survival (p < 0.05) and ocean effects were therefore estimated after adjusting for weight-at-release. Negative survival trend was modeled for sea surface temperature (SST) during 11 months of the year over the study period (1970-1992). Statistically significant negative survival trends (p < 0.05) were found for SST during April, June, November and December. Strong pairwise correlations (r > 0.6) between SST in April/June, April/November and April/December suggest the significant relationships were due to one underlying process. At higher latitudes (45° and 48°N), summer upwelling (June-August) showed positive survival trend with survival and fall (September-November) downwelling showed positive trend with survival, indicating early fall transition improved survival. At 45° and 48°, during spring, alternating survival trends with upwelling were observed between March and May, with negative trend occurring in March and May, and positive trend with survival occurring in April. In January, two distinct scenarios of improved survival were linked to upwelling conditions, indicated by 1) a significant linear model effect (p < 0.05) showing improved survival with increasing upwelling, and 2) significant bowl-shaped curvature (p < 0.05) of survival with upwelling. The interpretation of the effects is that there was (1) significantly improved survival when downwelling conditions shifted to upwelling conditions in January (i.e., early spring transition occurred, p < 0.05), (2) improved survival during strong downwelling conditions (Bakun units < -250). Survival decreased during weak downwelling conditions (Bakun units between -180 and -100). Strong to moderately strong correlations between January upwelling and April SST (r = 0.5), June SST (r = 0.6), and the North Pacific Index (NPI) of Aleutian Low strength (r > 0.5) 0.7) suggest January is a period when important effects originate and play out over ensuing months. Significant inverse trend with survival (p < 0.05) was found for Bakun indices in December, indicating strong downwelling improved survival.

Higher-than-average adult return rates were observed for cohorts from brood-years 1982-

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1983, strong El Nino years. Individual hatcheries were found to have unique age-class strengt	th
and age-at-return characteristics.	

## **Executive Summary**

#### **Study Objectives**

- To apply Ryding's (1998) multinomial-proportional hazards (MPH) model to analyze fall chinook salmon hatchery CWT data in order to identify oceanographic factors that may be affecting first ocean-year survival.
- 2. To determine optimal oceanographic conditions for the survival and return of fall chinook salmon.
- 3. To determine the relationship between the timing and size of releases of hatchery fall chinook salmon and ocean survival and adult returns.

#### **Accomplishments**

- Assembled CWT release and recovery data on fall chinook salmon from ten coastal hatcheries in Washington and Oregon for the years 1970 to 1992
- 2. Investigated 53 oceanographic covariates that might have been related to the early ocean survival of fall hatchery chinook salmon.
- 3. Identified several significant relationships between ocean covariates and release timing on the early marine survival of fall chinook salmon.

#### **Findings**

Weight-at-release had a significant effect on survival (p < 0.05) with survival improving with increased weight-at-release. Highly correlated with weight-at-release (r > 0.8), release month was also found to be significantly related to fall chinook salmon survival (p < 0.05) using a generalized linear model approach. Smolts released in summer to early autumn had higher return rates than smolts released in spring to early summer.

The MPH modeling approach was applied to ocean covariates after adjusting for weight-at-release, allowing oceanographic and release effects to be tested for significance separately. After adjusting for weight-at-release, several significant oceanographic effects were found. Negative trends between SST measured in every month of the year except January and survival was observed. Significant SST-months (p < 0.05) were April, June, November and December. A significant positive trend with survival (p < 0.05) was found with January upwelling at  $45^{\circ}$ . A signif-

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icant (p < 0.05) bowl-shaped curvilinear relationship was found between survival and Bakun indices (1970-1992), with best conditions occurring at the highest values (Bakun indices near zero, indicating spring transition), worst conditions occurring mid-range (Bakun indices between -180 and -80), and good conditions occurring in years of strong downwelling (Bakun indices < -250). Significant (p < 0.05) negative survival trend with December Bakun indices indicated survival improves with strong downwelling in December. Trends of upwelling at 45° and 48°N with survival included improved survival with increased upwelling in the summer months (June-August), improved survival with increased downwelling in fall months (September-November), and alternating survival trends in spring months, with increased upwelling having negative effect on survival in March and May, and increased upwelling having positive effect on survival in April. The northward extend of upwelling during June (JNUE) was found to have a significant downward effect on survival, indicating upwelling conditions that are too strong may be deleterious to survival.

Strong (r > 0.6) positive correlations between April SST and June SST, between April SST and November SST, and between April SST and December SST suggest the significant temperature effects were due to a common underlying process, rather than two or more local ones. Strong to moderately strong correlations involving January upwelling and April SST, June SST and the North Pacific Index (NPI) suggest January may be a period of important effects which play out in the ensuing months.

#### **Management Implications**

New NMFS conservation hatchery initiatives will require details on rearing practices such as those reported here relating release timing and size to subsequent survival, in order to manage hatcheries for long-term stock viability. Accurate and precise estimation of oceanographic effects on hatchery stocks will depend on adjusting for effects due to hatchery practices. Many Pacific Northwest ESUs are composed largely of hatchery-supplemented fish, making their survival relationships, age-at-return and age-class strength characteristics essential to our knowledge on the ESUs.

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Investigating survival relationships of individual hatchery stocks provides the information at geographic scale appropriate to the current state of Pacific Northwest salmon oceanography. Understanding small- and meso-scale processes of production, predation and bioenergetics will depend in part upon the cumulative understanding of many local relationships between survival and global/basin-scale effects.

Proper management of the salmonid resources of the Pacific Northwest depends on reliable scientific information and this research provides additional evidence for the scientific value of the modeling approach used here and in Ryding and Skalski (1999). One strength is the ability to model age-one survival estimates upon covariates measured during actual time of entry into marine habitat. Because age-one survival is an indicator of cohort strength, basing estimation on pinpointed entry conditions may increase the accuracy and precision of estimates compared to other models. In addition, the model does not require estimates of catch-effort, and this dispenses with an additional layer of variability. These considerations together may be of particular advantage for data with high variability and many gaps, such as CWT data.

#### **Recommendations for further research**

Perform a follow-up study on CWT marked steelhead trout rear in coastal hatcheries of the Washington and Oregon coasts. Investigate spring transition date as a covariate that may have a significant relationship with early marine survival of fall chinook salmon and steelhead trout.

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## 1.0 Introduction

"Salmon Oceanography?" (Wooster 1997) was the keynote address to the 1996 NMFS Workshop on Estuarine and Ocean Survival of Northeastern Pacific Salmon. The question behind the term was whether or not three decades of interdisciplinary research bridging the gap between oceanography and salmonid population biology, would someday mature into a separately recognized scientific discipline. Wooster's talk underscored how recently evidence of globally-synchronized, interdecadal-scale variability in marine populations has brought oceanographic effects into prominent focus in the discussion of Pacific Northwest salmon stocks (e.g., Yoder et al. 1999, Anderson 2000, Noakes et al. 1998). Processes of North Pacific salmon oceanography are commonly divided into three scales of effects, small-, meso-and global/basin-scale<sup>1</sup> (Brodeur and Peterson 1997). It is estimated (Yoder et al. 1999) that the small- and meso-scale processes, the media through which larger processes effect change, are at best decades from being fully understood. Yet a small number a familiar variables form the core of global/basin-scale research. These variables are believed to influence water column or marine ecosystem properties which affect food availability for salmon, predation on salmon, and salmon bioenenergetics. They include sea surface temperature, salinity, indices of river plume formation, broad climatic indices which characterize dominant weather patterns (e.g., El Nino-Southern Oscillation or ENSO events and Aleutian Low pressure intensity), and a handful of indices which measure coastal upwelling, including Bakun indices, spring and fall transition dates, and wind vector components. This study is in this category of research, and investigates the effects of selected global/basin-scale variables thought to affect survival of fall chinook salmon.

The primary objective of the study is to add to the body of knowledge bridging the gap toward understanding local causes of population fluctuations of salmonid stocks whose viability is of concern. The specific goals of this study were to identify oceanographic factors affecting the survival of fall chinook salmon from Oregon and Washington during their first year in marine habitat, and, if possible, to identify the forms of the relationships between these covariates and first-year survival. To focus on the marine phase of fall chinook salmon life history, the study used

<sup>1.</sup> Small-scale processes operate within 1 kilometer, in time frames of minutes of hours, meso-scale within 100 kilometers in days or weeks and global/basin-scale processes operate in time frames from annual to paleo.

coded wire-tag (CWT) release/recovery data from coastal hatcheries. To focus estimation of survival on the first ocean-year, a multinomial likelihood model was used to partition age-class strength, and age-one survival was modeled as a proportional hazards regression of survival against covariates. Moreover, because many of the ocean covariates used in the study were measured monthly, the modeling approach effectively pinpoints first-ocean year survival to first months at sea. Beyond the stated goals there was additionally an interest in evaluating the quality of CWT data. Healey (1991) described this 30+-year archive as a "wealth of historical data... [which]... remains completely unanalyzed", presumably because of questions about its quality (Chapter 2, Section 2). A number of studies have been carried out since Healey's observation (e.g., Coronado-Hernandez 1995, Hyun 1996, Mahnken et al. 1998, Ryding and Skalski 1999) which affirm its value for purposes of scientific discovery.

This study is a follow-up to Ryding (1998), extending the application from coho salmon to include fall chinook salmon. In addition to evaluating the climate indices studied by Ryding (the Pacific Northwest Index, PNI and the North Pacific Index, NPI), this study extended the investigation of summertime sea surface temperature (SST) and Bakun coastal upwelling indices to include measurements from all twelve months, an extension necessitated by the unique features of fall chinook salmon life history. The remainder of this introduction is divided into three sections intended to supply relevant and necessary background into the oceanographic covariates studied, the survival data used, and the life history of the fall chinook salmon, in that order.

## 1.1. Salmon Oceanography

Recent examples of decadal-scale variability in marine populations include a 70% decrease in zooplankton biomass observed in the California Current since the 1950s, and a concurrent increase of up to 100% in zooplankton biomass and populations of pelagic nekton (e.g., salmon, squid) in the Alaskan gyre (Brodeur and Ware 1992, Beamish and Boullion 1993). It is now commonly held that such large swings in populations are examples of normal decadal-scale growth or decline in marine ecosystems. Initial evidence was derived from deposits of fish scales in sediments which indicated extreme fluctuations in population sizes in some fish populations long before the advent of large-scale fishing (Baumgartner et al. 1992, Yoder et al. 1999). It is now

known that populations of small coastal pelagic fishes such as anchoveta (herbivorous anchovies, sardines, and sardinellas) which support many of the largest fisheries in the world, are particularly prone to wide population swings and fishery collapses (Yoder et al. 1999).

The opposing growth trends in the California Current/Alaskan gyre populations since the 1950s are believed to exemplify oceanwide synchronies in fluctuations of pelagic fish populations, which are either in-phase or directly out of phase with each other. Two of the largest coastal pelagic fish populations of the world, the Peruvian anchoveta and the South African sardine, appear to rise and fall directly out of phase with the Pacific sardines (Yoder et al. 1999). In the northeast Pacific Ocean, Welch (1997) noted opposite survival trends in northern and southern British Columbian steelhead stocks and Mahnken, et al. (1998) observed that hatchery fall chinook salmon from the north and south of Puget Sound displayed opposite survival trends.

Large-scale fluctuations in fish populations are driven by climatological "forcings". Spencer and Collie (1997) identified, by cluster analysis, six categories of fish population fluctuations worldwide and showed that these patterns could be simulated by simple multiple-equilibrium models varying only in amplitude of environmental variability and intrinsic growth rate. Noakes, et al. (1998) demonstrated the close, in-phase tracking of time series of Air Circulatory Indices (ACIs) and of all-country catches of sockeye, pink and chum salmon in the northern Pacific from 1926-1995. Out-of-phase cycles have been observed between Columbia River spring chinook salmon catches and time series of the Pacific Northwest Index (PNI, a climatological index, Ebbesmeyer and Stickland, 1995) between 1935 to 1995 (Anderson 2000). Mantua (1997) showed correlations between salmon production trends and the Pacific Decadal Oscillation (PDO). Negative correlation has been demonstrated between U.S. West Coast salmon production and the strength of the Aleutian Low pressure front based on the North Pacific Index (NPI, Trenberth and Hurrell 1994) and the Aleutian Low Pressure Index (ALPI, Beamish 1993).

The large-scale climatic indicators mentioned in the above paragraph characterize, in one way or another, the two phenomena that dominate the climate and weather conditions of the northeast Pacific Ocean, the Aleutian Low pressure front in the Alaskan gyre, and the coupled ocean/atmospheric currents known as ENSO (El Nino/Southern Oscillation) events. Coastal winds are driven by the Aleutian Low pressure front in the Alaskan gyre. This front dominates the

weather of the northeast Pacific Ocean by intensifying or weakening two major atmospheric currents, the Subarctic and Alaskan Currents, which subsequently affect a third, the California Current. Strong El Ninos, occurring roughly every 20 to 25 years, are thought to be the "driving engines" of the decadal-scale forcings affecting salmon ecosystems of the Pacific (and as part of the effect of the world's largest ocean on other oceans, ENSO may play a primary role in their ecosystems as well, Yoder et al. 1999). The El Nino current propagates eastward along the equator from the western Pacific as an equatorially-trapped pressure cline. Heat is carried in the current and there is also a rise in sea level. After El Nino encounters the coast of the Americas, the current divides, the branches moving toward either pole. Strong El Ninos continue to the mid-latitudes (30 to 50 degrees), carrying an extreme of heat to those waters. El Nino also affects the strength of coastal winds along Washington and Oregon as well as relationships between upwelling and production.

Each year, along the Pacific Coast between San Francisco (38°N latitude) and the Queen Charlotte Islands (52°N), the coastal winds switch from the southerly (northward) winds of winter to the northerly winds of summer producing a transition in wind called the spring transition. Strong wintertime Aleutian Low pressure fronts pull the easterly Subarctic Current north, which in turn increases the southerly Alaskan Current. The effect of this is to weaken the northerly upwelling winds of the California Current, which blow south along the west coast of Washington, Oregon and California during summer. West Coast salmon production decreased after a significant 1976-77 climate shift from a period of weak Aleutian Lows to a decades-long intensification of the Aleutian Low. It is believed that West Coast salmon production thrives when weak Aleutian Lows induce strong summer upwelling winds because these winds bring an upward flux of micronutrients (phosphates, nitrates, etc.) into the surface layers of the ocean. This wind-driven vertical mixing induces primary production (production of phytoplankton through photosynthesis) and feeds the nearshore food chain.

El Nino affects the strength of coastal winds and production, but in complex and unpredictable ways. Coastal upwelling was anomalously low off California in early 1983 (a strong El Nino year). However upwelling was higher than normal off Peru, at the same latitude south as California is north. Even so, nutrient inputs to the surface layer off Peru were low, indicating the nutri-

cline during El Nino was deep beyond the effects of coastal upwelling. Substantial negative impacts on adult salmon production were observed during strong El Nino years 1982-83 (Brodeur 1997). However returns of CWT-marked subyearling fall chinook salmon from the 1982 and 1983 brood-years were observed higher than average (Hyun 1996, Mahnken et al. 1998).

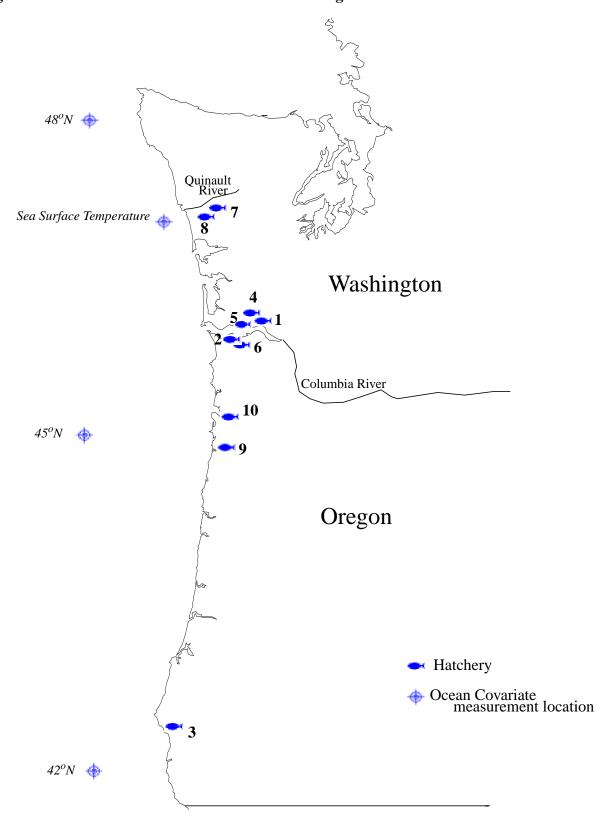
Much research in Northeast Pacific salmon oceanography has focused on two indices characterizing the effects of the Aleutian Low and ENSO events, the Bakun index of upwelling/downwelling and sea surface temperature. Bakun indices, available through the data center maintained by the National Oceanic Atmospheric Association (NOAA), are calculated from surface wind shear measurements, made daily by the hundreds, from NOAA observation ships. They are not based on measurements taken within the water column, but are instead related to Ekman transport. Ekman transport is a displacement of surface waters 90 degrees to the right of the wind direction<sup>2</sup>. It is measured by wind stress divided by the Coriolus parameter, which is computed from the earth's rotation and tilt. In the Northeast Pacific, Ekman transport driven by winds moving southward and parallel to the shore displaces surface waters away from the coast. The displaced waters are replaced by cooler, higher-salinity, nutrient-rich waters from 50-100 meters below the surface (www.cbr.washington.edu/dart.html, second-tier database to NOAAs PFEL database). It has been estimated that primary production is roughly proportional to Ekman transport (Ware and Thompson 1991).

I used monthly averages of Bakun indices based on daily recorded measurements taken from three areas off the coast, at 42°, 45°, and 48° North latitude (Figure 1.1), from 1970 to 1992. Positive values of Bakun indices indicate upwelling (seen in summer) and negative values indicate downwelling conditions (caused by southerly coastal winds, seen in winter). Large absolute values of the Bakun index indicate stronger vertical movement of water driven by wind.

The way in which primary production and other lower trophic-level processes in tropical to mid-latitude shelf ecosystems respond rapidly and dramatically to wind-driven upwelling is dauntingly complex (Yoder et al. 1999). While many studies have contributed to our knowledge of the effects of coastal upwelling on salmon stocks (e.g., Gunsolus 1978, Scarnecchia 1981, Nichol

<sup>2.</sup> This is true in the Northern hemisphere. In the southern hemisphere it is displacement 90° to the left.

Figure 1.1 Hatcheries and ocean covariate measuring sites.



son and Lichatowich 1984, Nickelson 1986) a thorough understanding the mechanisms of the nutrient supply to the water column is still decades away (Yoder et al., 1999). Gunsolus (1978), Scarnecchia (1981), Nicholson and Lichatowich (1984) and Nickelson (1986) found positive correlation between cumulative upwelling<sup>3</sup> and salmon survival; Fisher and Pearcy (1988) found positive correlation between cumulative upwelling and salmon growth rate. Ecological and conceptual models combined with many more studies are essential to gain understanding of how advective forces combine with eddies, jets and riverine plumes to affect upwelling, and how these physical features affect the biological and chemical processes involved in new and primary production. The Columbia River plume adds a level of complexity to the marine ecosystems off the Washington and Oregon coasts. The plume itself is subject to variation in size, shape, and location depending on the timing of spring transition and the strength of prevailing winds, which depend on climatic forcings such as dictate wind strength and direction. The plume may provide a benign transitional habitat for recent migrants (Brodeur and Peterson 1997).

Food-chain structures arising from inter-relationships between water column properties, lower trophic level production, predation, and salmon survival are also not well-understood. Whether decreased survival during weak upwelling years is caused by increased abundance of predators or by decreased growth rate of juveniles encountering nutrient-poor habitat, or both, is not clear. Nor is it clear how increased predator abundance might be related to upwelling. It is not known whether decreased juvenile growth rate increases mortality primarily through increased vulnerability to predation or through other causes (Brodeur and Peterson 1997). Brodeur and Peterson (1997) suggest that upwelling may affect salmon survival by providing a large coolwater habitat, or by providing favorable circulation patterns that are vital to salmon survival in some way, or by increasing the "complexity" of the continental shelf waters (Brodeur and Peterson 1997). Whether the interaction between winds, circulation, upwelling and productivity in April/May is more important for survival than the maximum zooplankton abundance in July/ August during strong upwelling years is unknown. The duration, frequency, and intensity of upwelling events affect survival (Cury and Roy 1989). Excessive upwelling-favorable winds may be detrimental to primary production if they cause nutrient-rich waters to be continuously advected offshore (Small and Menzies 1981). Pulsed upwelling conditions produce higher levels

<sup>3.</sup> Total cumulative upwelling from May to September.

of biological productivity in shelf waters (Brodeur and Peterson 1997). However, optimal pulse frequencies, if they exist, are unknown. Brodeur and Peterson (1997) observed that the Bakun index has shed little light on coho growth or survival since the regime shift of 1977-78. On the one hand this may be a call to recalibrate the index and maximize the signal-to-noise ratio during different climatic regimes. On the other hand, if the biological response in nearshore waters is due to local winds and eddies, then the upwelling index, being a function of large-scale dynamics, may be providing little useful information. In addition, different species exhibiting large differences in length of estuarine rearing, would be expected to exhibit unique responses to effects measured by Bakun indices.

If the Bakun index proves its worth for quantifying fundamental survival relationships, it will be through conceptual models such as Gargett's (1997) optimal window theory. The pivotal construct of this theory of production in the Northeast Pacific is water column stability. Under optimal conditions, water column stability allows for both deep infiltration of sunlight and upwelling of nutrients, and photosynthesis is maximized. Excessive stability (insufficient wind, vertical mixing) produces a situation where nutrients are the limiting factor. Insufficient stability (excessive wind, turbulence) produces a situation where the limiting factor is sunlight. Optimal windows of water column stability will occur in different times and locations in the Northeast Pacific Ocean depending on the strength of the Aleutian Low pressure front. The Bakun index would be an important measure in this constellation of effects. Ryding and Skalski (1999) reported evidence of an optimal window for coho survival in their model fitted curves of survival against June SST. Several by-hatchery fitted curves were markedly similar in shape and more markedly similar in their maximum survival temperature. Each curve peaked at approximately 13.5° Centigrade. Because upwelled water is colder than offshore water of the same latitude, these results were interpreted to mean that temperatures below approximately 12°C indicate conditions of excessive vertical mixing brought about by intense winds, and temperatures above 14°C indicate conditions of excessive water column stability, where winds are too weak to produce sufficient nutrient upwelling.

The June temperature limits on optimal coho survival defined by the Ryding and Skalski (1999) models may not be merely indicators of an optimal "Gargett-window", but bioenergetic

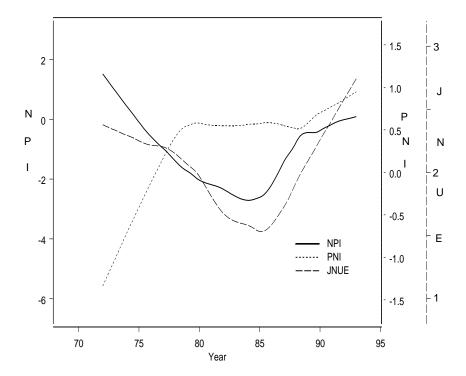
causes themselves, as research by Welch (e.g., 1997) suggests. Through research begun in 1990, Welch reports finding extremely sharp thermal limits on the ocean distributions of all salmon species in the North Pacific Ocean, with abundances dropping by one or two orders of magnitude in approximately 1°C. Welch asserts that "the primary control on salmon distribution is temperature", but that the upper thermal limit varies throughout the year, with a different limit every month. In a sense each species defines itself through the unique thermal limits on its ocean distribution. A hypothesized causal mechanism is that bioenergetic effects of increased water temperature forces juveniles to increase their foraging time, increasing their susceptibility to predation (Welch 1997, Brodeur 1997). Other studies advancing SST as directly causal to survival refer to a wintertime "preconditioning" (Logerwell 2000), whereby the temperature effect, in unknown ways favorably influences growth or survival in subsequent months. For example, Dickoff et al. (1989) found that Atlantic salmon reared in ambient winter temperatures as opposed to heated water survived better, and concluded that warm water temperatures in winter may be detrimental to subsequent survival. Hyun (1996) found significant negative correlation between winter (October through January) SST off Canada and fall chinook salmon survival and found higher juvenile growth rate in colder years. SST off Canada had the most significant effect on survival of all the oceanographic factors tested, including Bakun upwelling indices, N-S components of wind vector, Columbia River flow at Astoria, or spring transition date (Hyun 1996). Match/mismatch hypotheses may also explain why survival is more affected by temperature during some months than others (Nickelson 1986, Ryding and Skalski 1999). An example of a match/mismatch scenario would be when a crucial foraging opportunity is missed because temperatures simultaneously present a bioenergetic peril to salmon or to prey. Nickelson (1986) reported that in years of strong upwelling conditions, survival was negatively correlated with June SST. Other SST studies found negative correlations between coastal SST and first ocean-year survival in chinook and coho salmon (Holtby and Scrivner 1989) and increased year class abundance of sablefish after extended periods of below average SST off Vancouver Island (McFarlaine and Beamish 1992). Sea surface temperatures are measured from ocean-moored buoys by the NOAA, and the data is available at the NOAA website. We used monthly averages of SSTs taken off Cape Elizabeth from buoy number 46041 (www.cbr.washington.edu/dart.html, second-tier database to NOAA PFEL) (Figure 1.1).

The Pacific Northwest Index (PNI) is an annual measure of climate in the Pacific Northwest. It reflects climate conditions and patterns in Washington State, both inland and on the coast. It is a yearly composite index developed by Ebbesmeyer and Strickland (1995) and uses three parameters from different locations in Washington, are 1) snowpack depth at Paradise on Mount Rainier on March 15th, 2) total precipitation at Cedar Lake, and 3) the average air temperature at Olga in the San Juan Islands. The index is an average of the standardized values of the three parameters. Negative values signify a cooler, wetter than average year, and positive values indicate a warmer, dryer year. PNI values for the period from the earliest CWT release in the study, 1972, to the latest CWT release, 1993, ranged from a low of -1.39 (cool and wet) to a high of 1.42 (warm and dry), with an mean of 0.27 (Figure 1.2).

The North Pacific Index (NPI) was developed by Trenberth and Hurrell (1994) and reflects annual changes in the intensity of the winter Aleutian Low pressure system. It is an average of sea level pressure in the area from 30 to 60°N and 160° E to 140° W, for the months November through March. Lower values imply lower mean sea level pressure over this area. Values range from a low of -5.82 millibars (mb) to 2.25 mb for the period 1972 to 1993, with a mean of -0.9383 mb (Figure 1.2).

A measure devised by Ryding and Skalski (1999), the June Northward Upwelling Extent (JNUE), measures the annual northward extent of upwelling during the month of June. During the winter months, downwelling (negative Bakun indices) occurs off the coast of Washington and Oregon, and changes to upwelling (positive Bakun indices) in the spring. While parts of coastal Washington or Oregon coast experience upwelling, downwelling continues throughout the summer along the coasts of Southeastern Alaska, British Columbia and the north of Washington state. A value of one (1) signifies upwelling extending as far north as the 48th parallel in June, a value of two (2) signifies upwelling was observed as far north as the 51<sup>st</sup> latitude (the northern tip of Vancouver Island, B.C.) in June, and a value of three (3) signifies upwelling extending to the 54th parallel, in June (Figure 1.2).

Figure 1.2 Loess-smoothed plots of three climate indices, plotted simultaneously against year from 1972-1994. Included are the Northwest Pacific Index (NPI, solid), the Pacific Northwest Index (PNI, short-dashed), and the June Northward Upwelling Extent (JNUE, long-dashed).



## 1.2. Hatchery CWT Data

The data analyzed were obtained from the Pacific States Marine Fisheries Commission's (PSMFC) coded-wire tag (CWT) database, maintained by the PSMFC's Regional Mark Information Service (www.rmis.org). Each year, hatcheries tag a percentage of juvenile salmon with CWT tags, which are designed to remain implanted for life. Coded wire tags are 1mm sections of wire encoded with a binary number, and implanted into the nasal cartilage of juvenile fish in order to track movement and survival patterns. The binary code on the tag identifies the fish to a release group, or batch. The CWT data includes date of release, date of recovery, and age at recovery so that when counts are eventually tabulated, recovery rates become available by age. While more than thirty years of CWT data exists in the PSMFC RMIS database, it remains, for the most part, unanalyzed (Healey 1991). In the last decade, however, several analyses of CWT data have been profitably carried out. Coronado-Hernandez (1995) performed an extensive analysis of hatchery

CWT data from Washington, Oregon, Idaho, California, Alaska and British Columbia. She investigated hatchery rearing effects on salmonid survival. Hyun (1996) used CWT data to compare ocean distributions between two hatchery-reared fall subyearling chinook salmon stocks from different river reaches, and to test for ocean effects on survival. Mahnken, et al. (1998) used the Coronado (1995) data base in a study of historical survival trend in Pacific rim hatchery-reared salmon populations. Ryding and Skalski (1999) tested for ocean effects on first ocean-year survival of coho using CWT data from coastal hatcheries in Washington state.

The size of a batch or release group varies from thousands to tens of thousands. It is common for a hatchery to release several batches of a given species in a brood-year. Total returns by age per year are estimated from tags recovered in the commercial and recreational fisheries, and at the hatchery when adult fish return. The commercial fishery samples a fraction of each catch for adipose fin-clips, which signal the presence of a CWT. Heads of the fin-clipped fish are collected and sent to central locations in each state, where tags are retrieved. The number of recovered fish from a given batch is divided by the sampling fraction at catch. These expanded counts estimate the total expected fish caught from that batch and these per-batch estimates are summed over catches and batches to tabulate total recoveries (by age) by year. Tag returns from the recreational fishery are done on a voluntary basis; consequently, estimates of catch from this fishery are less accurate than commercial fishery and hatchery return estimates. There is higher variability in returns relative to variability in releases. Ryding (1998) suggested that survival estimates based on CWT returns will underestimate true survival since there are probably more tagged fish recovered than reported.

Subyearling fall chinook salmon reared in hatcheries in Washington and Oregon State are released from February through December, but most are released during June, July, and August. The hatcheries in this study released fish into coastal rivers or streams as early as April, and as late November. Because fish released in April are smaller than fish released in November, there is, predictably, wide variation in release weights. In this study the minimum average batch weight was 2 grams, and the maximum was 75 grams. The hatcheries located in Oregon release fish at larger weights, later in the year, than Washington hatcheries.

There were two criteria for hatchery selection for this study. Firstly, the hatchery should be located on or near the coast, so that the variability in survival could be attributed to marine as opposed to freshwater conditions. Secondly, each hatchery had to have release-recovery data for at least l+2 brood-years, l being the number of model parameters (Chapter 2). Ten coastal and Lower Columbia River hatcheries from Washington and Oregon met the data criteria (Table 1.1) and their locations are mapped in Figure 1.1.

Table 1.1: Hatcheries with CWT data used in this study.

Hatchery	Location ID in Figure 1.1
Abernathy	1
Big Creek	2
Elk River	3
Elochoman	4
Grays River	5
Klaskanine	6
Quinault Lake	7
Quinault NFH	8
Salmon River	9
Trask	10

None of the hatcheries in this study had fish returning over five years old. Although some populations of chinook salmon are known to have returning 9- and 10- year-old adults, this appears to be rare at this latitude. This may be due to the tendency for fish from more southerly latitudes in the Northeast Pacific to have older mean ages at return (Coronado-Hernandez 1995).

Table 1.2 shows the brood-years for which release and recovery data were available, for each hatchery. It is clear from the distribution of X's in the body of the table that many gaps exist in the data and that consequently, a brood-year effect may be confounded with other effects.

Table 1.2: Brood-years for which CWT release and recovery data were available for each hatchery. Shaded 'X's indicate release and recovery data were available for the given hatchery and brood-year.

brood					hato	cheries				
year	Aber- nathy	Big Creek	Elk River	Elo- koman	Grays River	Klas- kanine	Quinault Lake	Quinault NFH	Salmon River	Trask
70										X
71		X								
72										
73	X		X	X				X		X
74	X		X		X	X		X		X
75	X				X			X		
76	X	X		X	X	X		X	X	
77	X	X	X	X	X	X	X	X	X	
78	X	X	X	X	X	X	X	X	X	
79	X	X	X	X	X	X		X	X	
80	X	X	X	X	X	X	X	X	X	
81	X	X	X	X	X	X	X	X		
82		X	X		X		X	X	X	X
83		X	X				X	X	X	X
84		X	X		X			X	X	X
85		X	X	X	X			X	X	X
86		X	X			X	X	X	X	X
87		X	X			X	X	X	X	X
88		X	X	X	X	X	X	X	X	X
89	X	X	X		X	X	X	X	X	X
90	X	X	X		X		X	X	X	X
91	X	X	X	X	X		X	X	X	X
92	X	X	X	X	X		X	X	X	X

#### 1.3. Fall Chinook Salmon Life History

Many studies point to the first few months of ocean residence as the period in which most ocean mortality occurs (Matthews and Buckley 1976, Bax 1983, Nickelson 1986, Fisher and Pearcy 1988, Holtby et al. 1990, Francis and Hare 1994). While the first summer in the ocean is important to survival, the period shortly after ocean entry is perhaps the most critical to cohort survival, and is perhaps the time when cohort success is determined (Pearcy and Fisher 1988, Holtby and Scrivner 1989, Brodeur et al. 1992, Pearcy 1992, Beamish and Boullion 1993). It is still not known whether mortality rates are highest during the first few days at sea or are low but constant during the first few months, or whether this differs by species who have evolved different adaptive mechanisms to environmental conditions.

Chinook salmon (*Oncorhynchus tshawytscha*) are distinguished by their large size, rapid growth rate, and preference for larger prey at equivalent life stages compared to other salmon. Adults may reach a weight of 45 kilograms. All Oncorhynchus species are anadromous and semelparous (meaning they die after spawning once). Within this general life history strategy, chinook display a broad array of adaptive tactics, including subdivision in two races which vary substantially in their lengths of freshwater residence, ocean distributions, and fidelities to natal rearing grounds.

Fall-run or "ocean-type" chinook salmon (so-named because of the comparatively longer amount of time this race spends in the ocean), migrate to sea during their first year of life, normally within 3 months after emergence from spawning gravel. They spend most of their ocean life in coastal waters, and return to their natal river in the fall, a few days or weeks before spawning. Ocean-type chinook salmon appear to be native to North American only.

At the time of emergence from eggs, there is an extensive downstream dispersal of fry. For populations that spawn close to tidewater, this downstream dispersal carries the fry to estuarine nursery areas, sometimes within a few hours. Estuaries provide important nursery habitat for recently emerged chinook salmon fry. Ocean-type chinook salmon do not appear to be sensitive to photoperiod. That is, they do not require a period of lengthening days before migrating, as some other salmon do.

Subyearling, ocean-type chinook salmon fry migrants normally range from 30 to 45 mm in fork length, although they have been recorded as small as 20 mm and as large as 55 mm. Many fry migrants still have visible yolk and few have begun feeding. Mortality is believed heavy in downstream migration. Many of the fry of ocean-type chinook salmon that migrate downstream immediately after emerging from the spawning beds take up residence in the river estuary and rear there to smolt size. Chinook salmon fry have been observed abundantly in the Columbia River estuary during March and April, where the smallest fry were observed to avoid brackish water and were consistently associated with freshwater inflows to the estuary.

Estuarine food habits vary considerably from estuary to estuary and from place to place within an estuary (Healey 1991). In Fraser River marshes, chinook salmon fry less than 50 mm long had diets which were dominated by benthic detritivores, herbivorous zooplankton and terrestrial insects. Along the Oregon coast benthic amphipods and aquatic insects are the dominant food of juvenile fall chinook salmon. In general, chinook salmon appear to be opportunistic feeders in estuaries. Comparison of their diet with that of other similar-sized salmonids in the same area suggests chinook salmon prefer slightly larger organisms and that larval and adult insects as well as amphipods of various sorts are the preferred prey in the intertidal regions of most estuaries.

Many important questions about estuarine habitat, raised a decade and a half ago, remain unresolved, including the issue of carrying capacity limitations for juvenile salmon in estuaries (Simenstad 1997). Estuaries are difficult habitats to study because of the "pulsed" character of estuarine fish populations and their prey. It is difficult to couple high densities of preferred prey to high densities of juveniles in estuaries. The variability in arrival and departure times of different species, each with different preferred prey, the large, unexplained variability between estuaries with respect to dominant prey species, in spite of the fact that all estuaries' food webs are detritus-based, the lack of known correlations between estuarine and ocean survival, the confounding anthropogenic effects through time--all contribute to making this a very complex habitat to research. Indeed the overlap and coincidence of salmon with peak prey resource availability are likely to be "random and uncoupled" events (Simenstad 1997). Bird populations who feed heavily on smolts in estuaries and river mouths are thought to pose a serious predatory threat to salmon populations.

Ocean-type chinook salmon have probably adapted to rear in estuaries, unlike stream-type chinook salmon (Levings 1997), an adaptive feature that may serve to increase survival in ocean-type chinook salmon. Wild and hatchery fish have been observed exhibiting different behaviors in estuaries (Levings 1997). Hatchery fish have different nutritional backgrounds (Levings 1992), different image of what they recognize as prey (Brodeur et al. 1992), and different fleeing behavior in the presence of predators (Healey 1991).

The affinity of young ocean-type chinook salmon for sheltered waters is general throughout the range of chinook salmon, but there is also some offshore movement of these fish. The estuaries along the open coasts of Washington, Oregon, and California afford the only sheltered water habitat in these regions and subyearling chinook salmon fry may continue to rear there during the summer and autumn, provided the temperatures in these estuaries do not get too high. Periods of slow growth in the Sixes River estuary in Oregon have been attributed to seasonal high temperatures (Healey 1991 citing Reimers 1971 and Nelson 1985), and to high densities of juvenile chinook salmon in the estuary during that period, leading to increased competition for food. The rapid growth following a slow-growth period was attributed to a reduction in population size when larger fish moved away from the estuary; and to cooling temperatures, both events taking place in the fall. Evidence appears to confirm that chinook salmon fry grow more rapidly in the estuary than they do in the river (Healey 1991). Sheltered habitat is much more common along the British Columbia coast, where there may be less stimulus for young chinook salmon to remain in British Columbia river estuaries. In Washington and Oregon, young ocean-type chinook salmon remain in estuaries considerably longer than they do in British Columbia. Studies of estuarine residence suggested a maximum residence time of about 60 days, and an average residency of 20-25 days. Chinook salmon fry residence appears to be associated with two habitat types found in estuaries: areas of subtidal refugia and tidal channels with low banks.

Fry remain in the estuarine nursery areas until they are about 70 mm in fork length, after which they disperse to nearby marine areas. Fisher and Pearcy (1995) reported that in 5 years of sampling juvenile salmon off the coast of Washington and Oregon, from 1981-1985, subyearling smolts were rare in their catches, despite the larger spawning populations producing these smolts compared to those producing spring/summer yearling chinook salmon smolts in their sampling area, and they suggested subyearlings were distributed in shallow water inshore of their sampling.

Their largest catches of smaller chinook salmon (<130mm fl) were taken in the low salinity, high-temperature waters of the Columbia River plume. During spring transition, when the prevailing wind pattern switches to northerly winds, the plume moves south extending well offshore and south to central Oregon. Coastal upwelling changes the shape of the plume, pushing it offshore. The date of spring transition varies from late January to May. Fish who enter the ocean before or shortly after the transition encounter a turbulent and highly saline environment, whereas later migrants that enter into a well-developed plume enter a relatively benign environment and could gradually adjust to oceanic conditions. The plume probably provides an important transitional habitat to the high salinity of oceanic water. River plumes have higher concentrations of zooplankton prey relative to adjacent marine waters. A decrease in the volume of water exiting the Columbia River during peak outflow periods has been observed over the last several decades, which may affect the thickness and offshore extent of the plume (Brodeur and Peterson 1997).

Healey (1991) notes that catches of chinook salmon in their first ocean year declined in July, owing to high surface temperatures at this time. Catches increase again in August-September when surface temperatures are lower. He also notes that, in August and September sampling, young chinook salmon were distributed about equally north and south of the Columbia River mouth but were still most abundant close to shore.

As chinook salmon become larger and begin to inhabit deeper waters their dietary preference shifts to larval and juvenile fishes. Information about first ocean-year distribution comes from studies done with small-mesh purse seines off the coast of Washington and Oregon (Fisher et al. 1983, 1984). These devices only go to about 20 m deep. Research cruises, sampling with gillnet and longline on the high seas, also give results mainly about surface waters. Chinook salmon are probably under-represented in these samples because of their tendency to be distributed deeper in the water column than the other species of Pacific salmon (Healey 1991).

Ocean-type adult chinook salmon remain in coastal waters throughout their marine lives. Coastal chinook salmon stocks from southern Oregon (south of the Rogue River) recruit to Oregon and northern California fisheries. Oregon stocks from Elk River, and north, contribute to fisheries from Oregon to Alaska and follow the migratory patterns of Washington coastal stocks. Mammalian predation by sea lions and seals on who forage for adult salmon in river mounts may

present a serious risk (Emmett 1997), particularly since the 1970s. Ocean-type chinook salmon appear to have a strong fidelity to natal rearing areas, unlike stream-type chinook salmon. Spawning time depends on the latitude and the particular river. In general, the more northerly the stock, the earlier spawning occurs. In the Columbia River, spawning is in late September.

Hyun (1996) found that hatchery and wild stocks from Lyon's Ferry hatchery have indistinguishable ocean distributions, but that this is different from the ocean distribution of Priest River Hatchery. Hyun found differences in catchability and/or age-at-maturity between hatchery and wild fish from Lyon's Ferry hatchery (1996).

# 2.0 Statistical Methods

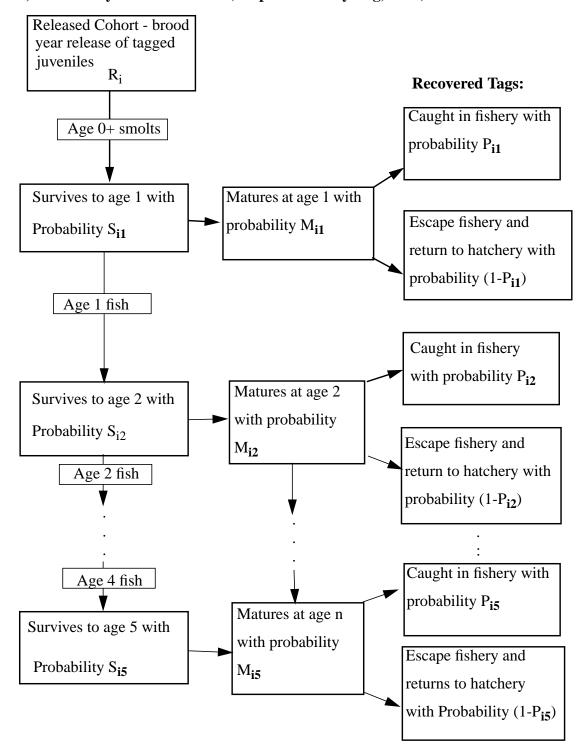
The statistical model used in this analysis of subyearling fall chinook salmon first ocean-year survival was a multinomial likelihood. The multinomial cell counts were the CWT age-class return numbers, and cell probabilities were constructed from age-class survival and maturity rates. First ocean-year survival was modeled as a proportional hazards regression on ocean and rearing covariates.

Figure 2.1 is a schematic representation of the process modeled by the multinomial probability distribution. A cohort of tagged juveniles is released as subyearlings (0+ years of age) from a hatchery. A proportion of the 0+-year-olds that survive into their second year (age 1+ fish) will mature as jacks and either return to their natal hatchery or be caught in the fishery. Those that are not recovered will, assuming survival a year hence, either mature and be recovered (by fishery or hatchery) as 2-year-olds, or remain in the sea, and so on.

A multinomial probability model was developed for the process depicted in Figure 2.1. Let the following variables be defined, where

- $R_i$  = the total number of coded-wire tagged smolts from brood-year i released from a hatchery,
- $O_{ij}$  = the number of tagged fish from brood-year i recovered in the fishery at age j,
- $H_{ij}$  = the number of tagged fish from brood-year i recovered at the hatchery at age j,
- $S_{ij}$  = the probability that a fish from the *i*th brood-year survives to the *j*th age-class, given it has survived to the (*j*-1)th age class,
- $P_{ij}$  = the probability a fish from brood-year i is caught in the fishery at age j,
- $M_{ij}$  = the probability a fish from brood-year i matures at age j.

Figure 2.1. A diagram showing the process modeled by the multinomial probability distribution, in the analysis of CWT data (adapted from Ryding, 1998).



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The expected number of one-year-olds recovered in the fishery or at the hatchery can be expressed as  $E(O_{i1}) = R_i P_{i1} S_{i1} M_{i1}$  and  $E(H_{i1}) = R_i (1-P_{i1}) S_{i1} M_{i1}$ , respectively. The expected number of combined one-year olds recovered is, then,

$$E(H_{i1} + O_{i1}) = R_i P_{i1} S_{i1} M_{i1} + R_i (1 - P_{i1}) S_{i1} M_{i1}$$

$$= R_i P_{i1} S_{i1} M_{i1} - R_i P_{ij} S_{i1} M_{i1} + R_i S_{i1} M_{i1}$$

$$= R_i S_{i1} M_{i1}$$
(EQ 2.1)

For two-years-olds, the expected number of recoveries in the fishery and hatchery, respectively, is  $E(O_{i2}) = R_i P_{i2} S_{i2} S_{i1} M_{i2}$  and  $E(H_{i2}) = R_i (1-P_{i2}) S_{i2} S_{i1} M_{i2}$ , and so on. The oldest recoveries, at age five have combined expected recoveries

$$E(H_{i5} + O_{i5}) = R_i S_{i5} S_{i4} ... S_{i1} M_{i5}$$

where 
$$M_{i5} = 1 - (M_{i1} + M_{i2} + \cdots + M_{i4})$$
.

An important aspect of this modeling approach is that the fishing effort,  $P_{ij}$ , drops out of the equation. There is no need to calculate fishing effort in order to analyze the data, an advantage first formally observed in Ryding (1998).

On the fishing boats, fishermen examine a portion, f, of the catch, for tags (they look for adipose fins clips, signifying presence of a tag). The number of clipped fins in the sample is divided by the sampling fraction, f, and this is referred to as the expanded count (or expanded recoveries) for that catch. We define  $t_{ij} = H_{ij} + O_{ij}$  as the expanded recoveries of fish from brood-year i that were recovered (in the fishery or hatchery) at age j.

The assumptions for the model can now be stated. They include universal assumptions about mark-recapture models as well as some assumptions that were specific to this model. The model assumptions include the following:

- Batches of coded-wire tagged fish are representative of the population of inference,
- 2) All tagged fish have an equal probability of surviving and migrating back to the hatchery in a particular year,
- 3) Release numbers of tagged smolts are known without error,
- 4) The numbers of recovered tagged fish for each tagcode batch are correctly reported,
- 5) Tagcode batch numbers are correctly identified,
- 6) Release groups are closed to emigration and straying is negligible,
- 7) Survival to the next age-class is constant across all years for a given stock from a given hatchery,
- 8) Maturation rate to a size or state of susceptibility to recovery is constant across all years for given stock from a given hatchery, and fish are not susceptible to recovery until they have reached that size/state,
- 9) Samples of fish examined for tags are representative of all the fish in the fishery (i.e., there is no bias toward or away from catching tagged fish),
- The fraction of fish sampled for computing expanded recoveries is known without error,
- 11) The fishery and the hatchery are the only places where tags are recovered.

Dropping brood-year subscripts for survival and maturation rates (Assumptions 7 and 8), the multinomial likelihood function can now be written as follows:

$$L(S_1, S_2, ..., S_5, M_1, M_2, ..., M_4 \big| \mathcal{R}_i, \mathcal{t}_{i1}, \mathcal{t}_{i2}, ..., \mathcal{t}_{i4}) = \prod_{i=1}^n \binom{\mathcal{R}_i}{\mathcal{t}_{ij}} (S_1 M_1)^{t_{i1}} \cdot (S_1 S_2 M_2)^{t_{i2}}$$

$$\cdot \left(S_{1}S_{2}S_{3}M_{3}\right)^{t_{i3}} \cdot \left(S_{1}S_{2}S_{3}S_{4}M_{4}\right)^{t_{i4}} \cdot \left(1 - S_{1}M_{1} + S_{1}S_{2}M_{2} + \dots + S_{1}S_{2}S_{3}S_{4}S_{5}M_{5}\right)^{-j = 1},$$
(EQ 2.2)

where  $M_5$  is equal to  $1 - (M_2 + M_3 + ... + M_4)$ . The parameters to be estimated are  $S_1, S_2, ..., S_5, M_1, M_2, ..., M_4$ , and  $R_i, t_{i1}, t_{i2}, ..., t_{i4}$  are the release and recapture data for each brood-year i.

Not all of the model parameters are estimable from the data for two reasons. The first is that several of the parameters always appear in conjunction with another parameter. The second is that there are two less sufficient statistics than parameters for each replicate. Both problems are solved by a model reparametrization, combined with the introduction of a covariate into the age-one cell probability.

The reparametrization decreases the number of parameters by one. It consists in defining parameters  $\theta_k$ , k=1,...,4 as  $\left(\prod_{s=2}^{k+1}S_s\right)M_{k+1}$  and  $M_5$  as  $(1-(M_2+M_3+...+M_4))$ . The resulting likelihood function is

$$L(S_1, M_1, \theta_1, \theta_2, ..., \theta_4 | \mathcal{R}_i, \mathcal{L}_{i1}, \mathcal{L}_{i2}, ..., \mathcal{L}_{i4}) = \prod_{i=1}^n \binom{\mathcal{R}_i}{\mathcal{L}_{ij}} (S_1 M_1)^{t_{i1}} \cdot (S_1 \theta_1)^{t_{i2}} \cdot (S_1 \theta_2)^{t_{i3}}$$

$$\frac{R_{i}-\sum_{j=1}^{4} t_{ij}}{(S_{1}\theta_{3})^{t_{i4}} \cdot (1-S_{1}M_{1}+S_{1}\theta_{1}+S_{1}\theta_{2}+\ldots+S_{1}\theta_{4})} .$$
(EQ 2.3)

The biological interpretation of the parameter  $\theta_k$  is now the probability of surviving and maturing at age k+1, given survival to age k. The parameters  $M_1$ ,  $\theta_k$ , k=1,...,4, are assumed constant across all brood-years for each hatchery.

The introduction of a covariate, which increases the sufficient statistics by one, is done in the form of the proportional hazards regression model. Age-one survival,  $S_1$ , is modeled as

$$S_1 = S_0^{e^{\overset{x'}{\Sigma}}}, \qquad (EQ 2.4)$$

where  $S_0$  is the baseline survival and x is an  $n \times l$  matrix of environmental covariates. The regression parameters,  $\beta$ , express the effect of the covariates on age-one survival. The PH model was chosen for its flexibility and its ease of parameter interpretation. Substituting the PH model for age one survival into the likelihood equation yields the final form of the likelihood model:

$$L(S_1, \beta, M_1, \theta_1, ..., \theta_4 \big| \underline{\mathcal{R}}_i, \underline{\mathcal{t}}_{ij}, \underline{\mathcal{X}}) = \prod_{i=1}^n \left( \underbrace{\underline{\mathcal{R}}_i}_{\underline{\mathcal{t}}_{ij}} \right) \left( S_0^{e^{\underline{\mathcal{X}}'\beta}} M_1 \right)^{t_{i1}} \cdot \left( S_0^{e^{\underline{\mathcal{X}}'\beta}} \theta_1 \right)^{t_{i2}} \cdot \left( S_0^{e^{\underline{\mathcal{X}}'\beta}} \theta_2 \right)^{t_{i3}} \cdot ...$$

$$\left(S_0^{e^{X'\beta}} \theta_3\right)^{t_{i4}} \cdot \left(1 - S_0^{e^{X'\beta}} (M_1 + \theta_1 + \dots + \theta_4)\right)^{R_i - \sum_{i=1}^4 t_{ij}} .$$
(EQ 2.5)

The PH model is equivalent to  $h(t) = h_o(t) \exp(x^i \beta)$ , where h(t) is the hazard function (Lee, 1992). The hazard at time t is proportional to the baseline hazard  $h_0(t)$  through a function of the covariate,  $e^{x^i \beta}$ . The equivalence of the hazard ratio,  $\frac{h(t)}{h_0(t)}$ , with  $e^{x^i \beta}$  expresses the main model assumption, that the hazard ratio is independent of time, t. The assumption implies that the biological response is to the covariate, and not to other effects included in the passage of time. Also called the relative risk, the hazard ratio is the risk of mortality of an individual with covariate X = x compared to an individual with covariate X = 0. The interpretation of the regression parameter, x = 0, is that for positive values of x = 0 there is an increased risk of mortality for increased values of the covariate x = 0. Negative values of the regression parameter indicate a decreased risk of mortality for an increase in the value of the covariate. For example, a regression coefficient of x = 0.

 $1^{\circ}$  C higher temperature has  $\exp(-0.0992) = 0.906$  or 90.6% of the risk of mortality of a fish exposed to the  $1^{\circ}$  C cooler temperature.

The model has k+1 minimum sufficient statistics for k parameters:  $t_{i1}e^{x_i}$ ,  $t_{i2}e^{x_i}$ ,...,  $t_{ik}e^{x_i}$ , and  $t_{i1}$ ,  $t_{i2}$ ,...,  $t_{ik}$ . A greater number of minimum sufficient statistics than parameters requires iterative methods to solve for the MLE's. The model parameters,  $S_0$ ,  $\beta$ ,  $M_1$ ,  $\theta_1$ , ...,  $\theta_4$  were estimated by numerically maximizing the likelihood function, using the "Fletch" routine (Fletcher, 1970).

The amount of data for each hatchery limited the number of parameters it was possible to estimate in two ways. Firstly, a hatchery with strong 1-, 2-, and 3-year-old age-class returns, but near-zero 4- and 5-year-old returns, say, supports estimation of parameters for the first three age-classes (i.e.  $S_0$ ,  $\beta$ ,  $M_1$ ,  $\theta_1$ , and  $\theta_2$ ); whereas a hatchery with regular, strong returns for all five age-classes supports estimation of parameters for all five age-classes ( $S_0$ ,  $\beta$ ,  $M_1$ ,  $\theta_1$ ,  $\theta_2$ ,  $\theta_3$ , and  $\theta_4$ ). The reason for this is that the numerical algorithm would not converge if the model were fitted with near-zero age-class data. Secondly, the complexity of the PH regression models, that is, the number of covariates it is possible to include in the age-1 survival model, was limited by the number of brood-years of data available for a hatchery. If the simplest model required estimation of k parameters, it needed at least k brood-years of data. Because it is not good statistical practice to use all available degrees of freedom in estimation, there was a minimum requirement of k+2 years of data for any model to be estimated. That meant a hatchery with 9 brood-years of data, and five strong year-classes of recovery data, could estimate only one regression coefficient.

Probabilities  $S_0$ ,  $M_1$ , and  $\theta$  were constrained to values on the unit interval (i.e., 0 to 1) in the optimization routine by reparametrization using the logistic function,  $f(x) = \frac{e^x}{1 + e^x}$ , thus avoiding singularities and boundary values, 0 or 1.

Ideally the likelihood function should be a smooth convex function, with parameter estimates maximizing the likelihood. However, given the complex nature of the model, and the variability

of the data, the exact behavior of the model was difficult to determine, and some models simply failed to converge to any parameter estimates. Holding all but one parameter constant and examining the values of the likelihood function for different values of that parameter resulted in concave down curves that were often very flat at the peak, thus prompting the algorithm to sometimes converge on different estimates of the same parameter, if it were given different initial values. While some models would not converge, and some models produced unreasonable estimates. Most models, however, given reasonable initial values based on salmon biology, produced reasonable parameter estimates and swift model convergence. Occasionally a model produced regression coefficients with zero standard error, resulting in infinite values of z- or t- statistics. In these cases a very small value (0.00001) substituted. All covariates were standardized before analysis according to the formula

$$Z = \frac{x_i - \bar{x}}{\sqrt{s^2}}.$$

Hypotheses about the covariates,  $H_0$ :  $\beta=0$  versus  $H_a$ :  $\beta\neq 0$ , were tested at a significance level of  $\alpha=0.10$ , using the test statistic

$$Z = \frac{\hat{\beta}}{\sqrt{Va\hat{r}_{adj}(\hat{\beta})}}.$$
 (EQ 2.6)

where

$$Va\hat{r}_{adj}(\hat{\beta}) = Va\hat{r}(\hat{\beta}) \cdot \frac{\chi^2 df}{df},$$
 (EQ 2.7)

$$\frac{\chi^2 df}{df} = \sum_{i=1}^n \sum_{j=i}^k \frac{(t_{ij} - E(t_{ij}))^2}{E(t_{ij})},$$
and  $df = (k-1) \bullet (n-(k+1)).$ 
(EQ 2.8)

The maximum likelihood estimator of the variance of  $\hat{\beta}$ ,  $Var(\hat{\beta})$ , was adjusted to incorporate model over-dispersion (Aitkin et al. 1990: p.214, McCullagh and Nelder 1983: pp.80-84). The scale parameter (EQ. 2.8) is a measure of model over-dispersion, with over-dispersion occurring when the value was greater than one. This was the case in every model estimated.

A weighted t-test of the null hypothesis of no overall effect of a covariate on survival across hatcheries was performed. The weighted t-test statistic was computed as

$$t_{df} = \frac{\hat{\bar{\beta}} - 0}{\sqrt{\hat{Var}(\hat{\bar{\beta}})}},$$
 (EQ 2.9)

where

$$\hat{\vec{\beta}} = (X'\hat{W}X)^{-1}X'\hat{W}\hat{\beta}, \qquad (EQ 2.10)$$

and where X is a vector of ones,  $\hat{W}$  a diagonal matrix of weights equal to the inverses of the variances of the individual coefficients, and  $\hat{\beta}$  the vector of the estimated regression coefficients from the individual hatchery models. The variance was computed according to the formula

$$\hat{Var}(\hat{\bar{\beta}}) = \frac{\sum_{i=1}^{n} \hat{W}_{i} (\hat{\beta}_{i} - \hat{\bar{\beta}})^{2}}{(n-1) \bullet \sum_{i=1}^{n} \hat{W}_{i}}.$$
 (EQ 2.11)

Weighted means give more weight to regression coefficients that have higher precision and less weight to coefficients estimated with lower precision. The weighted t-statistic has a Student's-t distribution with df = n - 1 degrees of freedom. A significant t-test result was interpreted to mean that the effect of a covariate was consistent across all hatcheries. A significant result implied the covariate did have an effect on survival to age one.

A quadratic proportional hazards model is written as  $(S_0)^e \beta_1 x + \beta_2 x^2$ . A positive coefficient in the quadratic term indicates a convex survival curve, and a negative quadratic coefficient indicates a concave curve. The covariate value at the inflection point is given by  $-\frac{\beta_1}{2\beta_2}$ .

A significant quadratic term suggests a non-linear model is a better fit for the covariate than a model with a strictly increasing or decreasing relationship with the covariate. As with the univariate model, the significance of a covariate was based on the results of a weighted t-test of the mean

of the quadratic term across all hatcheries, testing the hypothesis  $H_0$ :  $\beta_2 = 0$  versus  $H_a$ :  $\beta_2 \neq 0$ . Statistical comparison of linear and quadratic models was based on likelihood ratio tests of the form

$$\chi_{df}^{2} = -2\ln\left(\frac{L_{A}}{L_{0}}\right), \qquad (Formula 2.12)$$

where the number of degrees of freedom is the difference in the number of parameters estimated by the likelihood model under the null (0) and alternative (A) models.

Final model evaluation was made on the basis of the chi-square goodness of fit criterion

$$\sum_{h} \sum_{i} \sum_{j} \frac{\left(t_{ijh} - E(t_{ijh})\right)^{2}}{E(t_{ijh})},$$
 (Formula 2.13)

where j indexes age-class, i brood-year, and h hatchery. Models with the smallest goodness-of-fit statistics, which were also found significant by the weighted t-test (Eq. 2.9) at  $\alpha=0.10$ , were chosen as the most significant covariates on fall chinook salmon survival. A model which is significant at the 0.10 level in the weighted t-test shows consistency of effect among the ten different hatchery effects. A model which ranks in the top twenty (out of fifty-three possible) models with respect to the goodness-of-fit criterion is one which minimizes the absolute difference between observed return rates and expected return rates under the model, regardless of the direction of individual hatchery effects. The intersection of the two select sets form the final group of significant model effects for the study.

# 3.0 Results

### 3.1 Age at Return

In this study, the multinomial-proportional hazards (MPH) likelihood model (Equation 2.5) was fitted to individual hatchery return-at-age data rather than combined-hatchery data pooled by age-class. The necessity of applying Equation 2.5 in this way can be appreciated after studying Tables 3.1 and 3.2, which show unique return-at-age characteristics for individual hatcheries. For example, Abernathy hatchery had strong returns of 1-, 2- and 3-year-olds recorded for all 13 brood-years of release-recapture data, with near-zero returns of 4- and 5-year-olds. Alternatively, Quinault Lake Hatchery recorded significant numbers of returns of 1-, 2-, 3-, 4-, and 5-year-olds for most years (Table 3.1). Table 3.2 displays tallies of strongest age-classes. Abernathy's strongest age-class was age-2 for each of the 13 brood-years studied (Table 3.2). By contrast, Quinault National Fish Hatchery's strongest age class was age-3 for 17 out of 20 brood-years studied (Table 3.2).

Table 3.1: Age-classes of strong adult return numbers, for each hatchery. 'X' indicates the age-class always had large returns. '0' indicates the age-class always had near-zero returns. 'M' indicates mixed results in age-class returns (see Appendix A for release and recovery data).

Ago					Н	latcheries				
Age Class	Aber- nathy	Big Creek	Elk River	Elo- koman	Grays River	Klas- kanine	Quinault Lake	Quinault NFH	Salmon River	Trask
age 3	X	X	X	X	X	X	X	X	X	X
age 4	0	X	X	M	M	M	X	X	X	X
age 5	0	0	M	0	0	0	X	M	X	M
age 6	0	0	0	0	0	0	0	0	0	0

Table 3.2: Largest returning age-classes for each hatchery and for all hatcheries combined. For example Abernathy's largest returning age-classes were 2-year-olds for each of 13 brood-years of data examined. Out of 149 brood-years examined for releases from 10 hatcheries, 67 showed the 3-year-old age-class as the strongest age-class.

Hatchery	Number of Brood-Years Having Age i as Largest Age-Class Return						
	age 1	age 2	age 3	age 4	total		
Abernathy	0	13	0	0	13		
BigCreek	0	15	3	0	18		
Elk River	0	3	13	0	16		
Elokoman	0	5	6	0	11		
Grays River	0	8	8	0	16		
Klaskanine	0	9	2	0	11		
Quinault Lake	0	0	6	8	14		
Quinault NFH	0	0	17	3	20		
Salmon River	1	1	6	8	16		
Trask River	0	1	6	7	14		
Combined Hatcheries	1	55	67	26	149		

## 3.2 Aggregation of CWT Tagcode Batches

The MPH modeling approach used brood-years as replicates, requiring the aggregation of tagcode batches by brood-year. This approach is justified by the results of a generalized linear model (GLM) pilot study (see Appendix D for details) which used tagcode batches as replicates. Both the MPH model applied to aggregated data, and the GLM applied to non-aggregated data, identified the same SST and upwelling months as accounting for most of the variability in adult return rates.

#### 3.3 Effect of Size at Release

Weight (in grams) of subyearling fall chinook salmon fry at the time of release was found to be a significant covariate influencing survival (see also Appendix D). Table 3.3 shows the results of the tests of linear effect of weight-at-release on first ocean-year survival using Equation 2.6. First ocean-year survival of subyearling fall chinook salmon fry released from Big Creek, Elokoman, Grays River, Klaskanine, Quinault National, and Trask hatcheries, as estimated by the MPH model was significantly affected by the weight at which they were released. Weight-at-release did

not appear to affect first-year survival of fry released from Elk River, Quinault Lake, and Salmon River hatcheries. The across-hatchery test of the effect of weight-at-release on survival showed the linear effect was highly significant, t = -2.79, with a p-value of 0.02.

Table 3.3: By-hatchery z-statistics for the test of the null hypotheses of no linear effect of weight-at-release on first ocean-year survival of subyearling CWT-marked hatchery fall chinook salmon. Shading indicates significance at alpha = 0.10.

Hatchery	z-statistic	p-value
Abernathy	-0.16	0.873
Big Creek	-7.60	0.000
Elk River	-1.40	0.162
Elokoman	-3.69	0.000
Grays River	-4.54	0.000
Klaskanine	-9.30	0.000
Quinault Lake	-0.31	0.757
Quinault NFH	-2.97	0.003
Salmon River	-0.25	0.803
Trask	-2.72	0.007

Because of observed curvature in many of the hatchery data plots of adult returns against weight-at-release (Figure 3.1), second-order regression models (models with both linear and quadratic terms, p. 28) were fitted.

Figure 3.1: Loess-fitted plots of weight at release (in grams) against total recovery fraction per brood-year, for each hatchery.

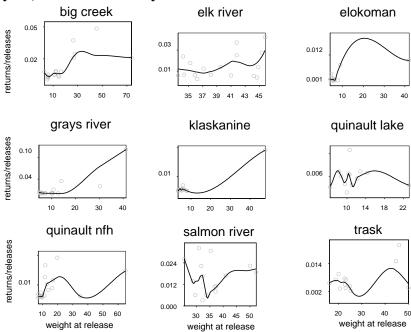


Table 3.4 presents the z-statistics for the test of no effect of weight-at-release in the second-order model. A significant quadratic relationship between weight-at-release and first year survival was in 5 of 10 hatcheries (p-value < 0.10).

Table 3.4: By-hatchery z-statistics for the test of the null hypotheses of no linear and no quadratic effects of weight-at-release on first ocean-year survival of subyearling CWT-marked hatchery fall chinook salmon. Shading indicates significance at alpha = 0.10.

Hatchery	z-statistic, linear term	p-values, linear term	z-statistic, quadratic term	p-values, quadratic term
Abernathy	0.12	0.904	0.32	0.749
Big Creek	-8.44	0.000	4.16	0.000
Elk River	-1.51	0.131	-0.94	0.347
Elokoman	-4.55	0.000	3.90	0.000
Grays River	-4.14	0.000	2.09	0.037
Klaskanine	-0.83	0.407	-0.11	0.912
Quinault Lake	-1.98	0.048	2.43	0.015
Quinault NFH	-3.79	0.000	2.55	0.011
Salmon River	0.57	0.587	-1.20	0.230
Trask	-1.00	0.317	-0.18	0.857

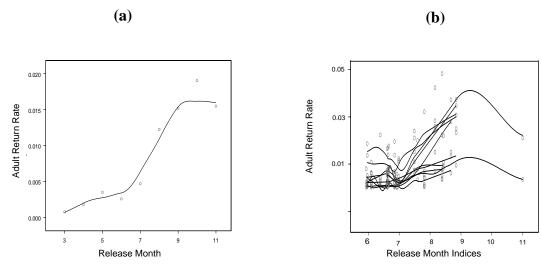
The across-hatchery test for effect of weight-at-release on survival showed a significant linear effect (t-statistic = -1.85, p-value = 0.1), and a marginally significant concave downward quadratic effect (t-statistic = 1.73, p-value = 0.12). The consequence of this analysis is that in modeling relationships between survival and ocean covariates, the effects of ocean covariates were examined after adjusting for Wt and  $Wt^2$ .

Time of release, which is highly correlated with weight at release (r=0.83), also influences adult return rate (Figure 3.2.a and 3.2.b). Figure 3.2.a shows the loess-smoothed plot of adult return rates plotted against release month. In Figure 3.2.a, returns from all hatcheries were pooled by release month. Figure 3.2.b shows hatchery-by-hatchery loess-fitted plots of adult return against release-month indices<sup>1</sup>. The combined hatchery data shows increased return rate with later release date, through September. Return rates increased (Figure 3.2.b) more or less monotonically with releases from July - September for all hatcheries. Return rates were about comparable when

<sup>1.</sup> Release month indices are calculated per brood-year as the weighted average of release months, with weights equal to batch releases.

releases occurred in June or July (Figure 3.2.b). Two hatcheries showed declining return rates when releases occurred after September (Figure 3.2b).

Figure 3.2: (a) Loess-fitted curve of total adult return rate by release month (March=3, April=4, etc.). For each release month return rates were averaged over batches (across hatcheries and years). (b) Loess-fitted curves hatchery-by-hatchery for adult return rates against release-month indices. Release-month indices are weighted averages of release month per brood-year.



# 3.4 Survival Relationships

Ryding's (1998) coho salmon study, which was a template for this study, included 11 ocean covariates: five annual measures of climatic conditions<sup>2</sup>, two measures of sea surface temperature (summer average SST and June SST), and four measures of local upwelling conditions (summer average Bakun indices at 45° and 48°N latitude and June Bakun indices<sup>3</sup> at 45° and 48°N). Relatively few covariates could be used to describe early ocean conditions for hatchery coho because they are all released over a rather narrow interval of time. On the other hand, hatchery subyearling chinook salmon were released from April to November from the hatcheries in this study. In addition to higher variability in release dates, subyearling fall chinook salmon fry also

<sup>2.</sup> North Pacific Index (NPI), Pacific Northwest Index (PNI), June Northward Upwelling Extent (JNUE), cumulative May through September monthly Bakun measures at 45° and 48° N.

<sup>3.</sup> Monthly SST and upwelling measures are averages of the NOAA daily measurements

have higher variability in their length of stay in estuaries, river plumes and protected coastal waters (Healey, 1991). As such, more numerous ocean covariates had to be investigated. In this study, 53 ocean covariates, including Ryding's five annual measures of climatic conditions and 48 monthly measures of ocean conditions, were investigated. Twelve of the 48 monthly variables were SST-months, or time series of SSTs recorded annually from 1970-1992, for each month. The remaining 36 monthly variables were upwelling-months, time series of Bakun indices, recorded over the period 1970-1992 for each month, at each of three latitudes, 42°, 45°, and 48° N. Appendix B includes tables of oceanographic covariates from 1970 to 1992.

For each of the ten hatcheries included in this study, first-year survival for subyearling fall chinook salmon was modeled using the relationship

$$S_{1} = S_{0}^{e} Mt + \beta_{2}Wt^{2} + \beta_{3}Cov + \beta_{4}Cov^{2},$$
(3.1)

where Cov is one of the 53 ocean covariates and Wt is the average weight-at-release from the hatchery<sup>4</sup>. By including Wt and  $Wt^2$ , the model partitions variability due to weight-at-release, leaving a truer picture of the variability accounted for by the ocean covariates.

Tables 3.5-3.8 and 3.10 display the results of the across-hatchery weighted t-tests (Eq. 2.9) for linear and quadratic effects of ocean covariates only, after adjustment for weight-at-release. Lightly-shaded cells signify the test was significant at the 0.10 level. Darker-shaded cells denote significance at the 0.05 level. Table 3.11 displays those significant covariates from Tables 3.5-3.8 and 3.10 which ranked in the top 20 best-fitting models according to the chi-square goodness-of-fit criterion (2.13). Column 2 of Table 3.11 summarizes the direction of significant effects. If a model had significant linear and quadratic terms, column 2 displays two symbols, one for the linear effect (either  $\uparrow$  or  $\downarrow$ ), and one for the quadratic effect ( $\bigcup$  or  $\bigcap$ ). A covariate having positive linear trend with survival is schematized as an arrow pointing upward ( $\uparrow$ ) and a covariate having a negative effect on survival (i.e., an inverse relationship with survival) is schematized as a down-

<sup>4.</sup> Wt is calculated as the weighted average of average batch release weights (in grams), where averaging is weighted by batch release size.

ward-pointing arrow ( $\downarrow$ ). A concave down quadratic effect, schematized  $\cap$ , is one which maximizes survival at some middle point in the range of its values. A concave up quadratic effect, schematized  $\cup$ , is one which maximizes survival at the high and low extremes of the range of covariate values, and which minimizes survival somewhere in the middle. Column 3 of Table 3.11 displays the level of the test for which a given effect is significant,  $\alpha = 0.05$  or  $\alpha = 0.10$ .

All four SST models with significant linear-term effects (April, June, November, and December SST) were among the top 20 best-fitting models (Tables 3.5 and 3.11). The linear-term t-statistics in SST-month fitted models (Table 3.5) are all positive but one, indicating that, in general, during years when sea surface temperatures were low, survival was high, and when temperatures were high, survival was low. This inverse relationship between temperature and survival was found for every SST-month except January, which had a negative sign in the linear term, indicating the opposite trend. The inverse relationship was found to be strongest (i.e., the negative slope of the regression line was largest, and variability was relatively small) during April, June, November and December. The model results suggest that temperature has a more profound effect on survival during these months than it does during other months.

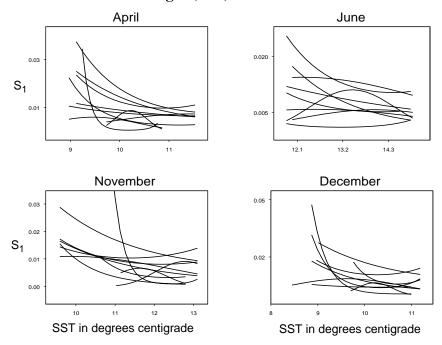
Fitted curves of the SST-month models identified in Table 3.11 are shown in Figure 3.3. April-SST shows a high degree of consistency among hatchery fitted curves in its display of downward survival trend with increasing temperature. The degree of consistency among hatchery fitted curves is not as apparent in the June-SST fitted curves (Figure 3.3). The explanation for this is that the across-hatchery test for effects (Eq. 2.9) is a weighted test, so hatcheries modeled with a smaller error variance are weighted more heavily, and it is the consistency of effects between the most accurate models (2.13) that are combining to produce significance in the weighted test result.

The fitted curves of the modeled effect of April SST on first ocean-year survival show a difference as high as a four-fold between survival probability for smolts exposed to 11°C and smolts exposed to temperatures of 9 to 9.5°C. The fitted curves modeling the effect of December SST on survival show that the chance of a smolt surviving in 9°C waters can be up to five times as good as the chance of a smolt in 11°C waters.

Table 3.5: Results of across-hatchery tests of effect for monthly SST. Lightly shaded cells indicate significance at  $\alpha=0.10$ , dark shaded cells significance at  $\alpha=0.05$ .

			Covariate Effect				
Ocean Covariate	Month	Lin	ear	Quad	Number of Hatcheries		
		t-statistic	p-value	t-statistic	p-value	Ή	
	Jan	-0.11	0.92	0.62	0.55	9	
	Feb	1.53	0.16	1.27	0.24	10	
Sea Surface Temperature (SST)	Mar	0.31	0.76	2.06	0.07	10	
lre (\$	Apr	4.83	0	-0.59	0.57	10	
eratu	May	1.57	0.15	1.72	0.12	10	
empe	Jun	2.88	0.02	-0.32	0.76	9	
e Te	Jul	0.94	0.37	0.91	0.39	10	
ırfac	Aug	1.71	0.12	2.56	0.03	10	
sa Sı	Sep	1.59	0.15	-1.25	0.25	9	
Se	Oct	1.78	0.11	-1.57	0.15	10	
	Nov	2.05	0.07	-0.98	0.35	10	
	Dec	3.32	0.01	-1.14	0.29	9	

Figure 3.3: Fitted curves from Eq. (3.1) of first-year survival,  $S_1$ , against SST. Equations evaluated at the mean value for weight (Wt).



The results of fitting Eq. 3.1 to Bakun indices are less consistent than the results of SST-month model-fitting<sup>5</sup>. Whereas all but one SST-month model between temperature and survival showed negative trend, nine 42°-upwelling-month models showed negative effect and three showed positive. At 45° and 48° N latitude, upwelling-month models showed half positive and half negative trend effects.

Only four of the 36 upwelling-month models were both significant and best-fitting, and three of those four were January- or December-upwelling models (Table 3.11). At  $42^{\circ}$  N latitude, December-upwelling, showed significant inverse trend with survival (Table 3.6, p-value = 0.02), in the linear term. At  $45^{\circ}$ , January upwelling showed significant trend with survival (Table 3.7, p-value = 0.08), and also significant concave upward curvature (p-value = 0.05). At  $48^{\circ}$ , December-upwelling again showed a significant inverse trend with survival (Table 3.8, p-value < 0.001).

<sup>5.</sup> Bakun indices measure coastal upwelling or downwelling and the general term "upwelling-month" refers to the time series, from 1970-1992, of Bakun indices recorded for a particular month. An upwelling-month, say June at 42°, fitted to the model, is referred to as the June-upwelling model.

Although January- and December-upwelling models were not both significant and best-fitting at any one latitude, the pattern of qualitative effects is so persistent at all three latitudes as to be worth noting (Tables 3.6-3.8).

To understand the relationship between increased upwelling and decreased survival, first consider Figure 3.4, which is a loess-smoothed plot of adult returns against January-upwelling, and Figure 3.5, which show model fitted curves for January and December upwelling at 45° and 42°, respectively. In December, conditions of downwelling prevailed for every year in the study period, 1970-1992 (negative Bakun indices indicate downwelling). Thus the interpretation of a "negative December-upwelling trend effect" is that survival decreases with decreased downwelling (negative Bakun indices become less negative). To say it another way, survival is better when there is

Table 3.6: Results of across-hatchery tests of effect for monthly Bakun indices at 42° N latitude. Lightly shaded cells indicate significance at  $\alpha=0.10$ , dark shaded cells significance at  $\alpha=0.05$ .

			Covariate Effect			Number Hatcheries	
Ocean Covariate	Month	Lin	Linear		Quadratic		
		t-statistic	p-value	t-statistic	p-value	ZH	
	Jan	-3.75	0	-3.43	0.01	10	
	Feb	0.28	0.79	0.44	0.67	10	
ses	Mar	0.18	0.86	0.37	0.72	10	
Indic	Apr	-1.52	0.17	1.76	0.12	9	
ing ] itude	May	1.3	0.23	-0.14	0.89	10	
ıstal Upwelling I. at 42° N latitude	Jun	0.49	0.64	-0.98	0.35	10	
I Up	Jul	0.91	0.39	-0.66	0.53	9	
asta at 4	Aug	-0.04	0.97	-0.35	0.73	10	
1 Co	Sep	1.74	0.12	0.19	0.85	10	
Bakun Coastal Upwelling Indices at 42° N latitude	Oct	1.4	0.2	-1.63	0.14	10	
	Nov	1.15	0.28	-0.09	0.93	10	
	Dec	2.85	0.02	0.13	0.9	9	

strong downwelling in December. With this observation made, the situation in January becomes clear also. Examination of the data plot for January (Figure 3.4) reveals two trends, one (i.e., left side of Figure 3.4) of increased survival due to increased downwelling and the other (i.e., right side of Figure 3.4) of increased survival due to decreased downwelling around Bakun index values of zero (downwelling is converting to upwelling, i.e., spring transition is occurring in January). Intermediate conditions (weak downwelling, Bakun indices around -100) have the worst effect on survival, as the bowl-shaped model curvature emphasizes (Tables 3.7 and 3.11). Of the two scenarios of enhanced survival (i.e., strong downwelling and spring transition), spring transition is best, as the fitted curves reveal (Figure 3.5) as well as the positive linear trend in the across-hatchery test (Table 3.7). The fitted curves for the effect of January-upwelling at 45°N (Figure 3.5) on first ocean-year survival show up to five-fold increase in survival probability for smolts exposed to transitional conditions, compared to downwelling conditions around -180 Bakun units.

Table 3.7: Results of across-hatchery tests of effect for monthly Bakun indices at 45° N latitude. Lightly shaded cells indicate significance at  $\alpha=0.10$ , dark shaded cells significance at  $\alpha=0.05$ .

		Covariate Effect					
Ocean Covariate	Month	Lin	Linear		Quadratic		
		t-statistic	p-value	t-statistic	p-value	Number Hatcheries	
	Jan	-1.96	0.08	-2.23	0.05	10	
	Feb	-0.33	0.75	-0.27	0.79	10	
ses	Mar	4.39	0	2.19	0.06	10	
Indic	Apr	-1.64	0.14	-0.3	0.77	10	
ing ing	May	1.32	0.22	1.82	0.1	10	
well latit	Jun	-0.76	0.47	-0.5	0.63	10	
oastal Upwelling at 45° N latitude	Jul	-2.02	0.07	-1.23	0.25	10	
asta ıt 45	Aug	-0.97	0.36	0.18	0.86	10	
1 Co	Sep	1.48	0.17	0.99	0.35	10	
Bakun Coastal Upwelling Indices at 45° N latitude	Oct	1.94	0.08	0.7	0.5	10	
	Nov	0.32	0.76	-1.49	0.17	10	
	Dec	6.48	0	-0.37	0.72	10	

Table 3.8: Results of across-hatchery tests of effect for monthly Bakun indices at 48° N latitude. Lightly shaded cells indicate significance at  $\alpha=0.10$ , dark shaded cells significance at  $\alpha=0.05$ .

			Covariate Effect				
Ocean Covariate	Month	Lin	Linear		Quadratic		
		t-statistic	p-value	t-statistic	p-value	Number Hatcheries	
	Jan	-1.39	0.2	-1.3	0.23	10	
	Feb	-0.88	0.4	-1.2	0.26	10	
ces	Mar	1.49	0.17	2.58	0.03	10	
Indi	Apr	-1.34	0.21	-1.21	0.26	10	
ling	May	1.65	0.13	0.54	0.6	10	
istal Upwelling I	Jun	-2.47	0.04	2.9	0.02	10	
11 U <sub>F</sub>	Jul	-0.38	0.71	-2.13	0.06	10	
oasta at 4	Aug	-1.16	0.28	-0.31	0.76	10	
n Cc	Sep	1.99	0.08	3.22	0.01	10	
Bakun Coastal Upwelling Indices at 48° N latitude	Oct	1.21	0.26	0	1	10	
	Nov	0.57	0.58	-0.71	0.5	10	
	Dec	3.69	0	-0.5	0.63	10	

Figure 3.4: Loess-smoothed plots of adult hatchery returns plotted against Bakun indices recorded from 1970-1992 during January at 45° N latitude.

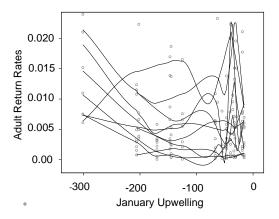
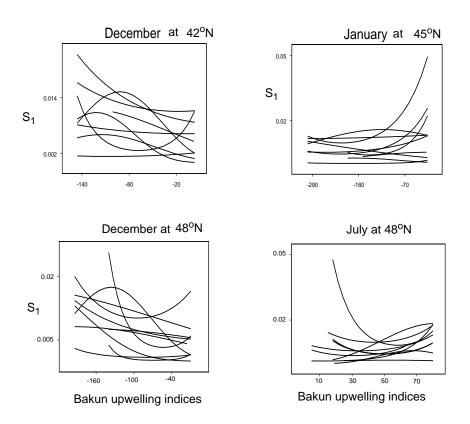


Figure 3.5: Fitted curves from Equation (3.1) of first-year survival,  $S_1$ , against Bakun upwelling indices at  $42^{\circ}$ ,  $45^{\circ}$ , and  $48^{\circ}$ N. Equations evaluated at the mean value for weight-at-release (Wt).



Note that latitude-by-latitude plots of Bakun indices track in-parallel during winter (solid lines, Figure 3.6), whereas, in summer there is separate tracking of Bakun index plots for different latitudes. Note also mirror-image relationships between SST (dotted) and Bakun indices (solid) in January and December, and the nearly linear increase in SST during July and August. The closer winter-time tracking of Bakun indices is also reflected in the between-latitude, within-upwellingmonth correlations, as one would expect. That is, inter-latitude correlations are higher during winter than during summer (Table 3.9, Table F3, Appendix F). This high correlation of wintertime downwelling dynamics results in the observed January/December effects at all three latitudes. By comparison, the upwelling/downwelling dynamics of spring, summer, and fall are more variable at each latitude.

Figure 3.6: Loess-smoothed plots of SST (dotted) and Bakun indices (solid) over the study period (1970-1992) for January, July, August, and December.

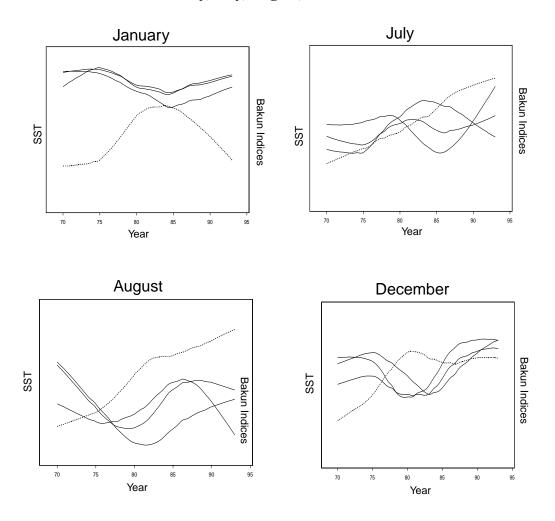


Table 3.9: Pairwise within-month correlations between Bakun upwelling indices at different latitudes.

Month	Correlations				
Monui	42°-45°	42°-48°	45°-48°		
May	0.86	0.60	20.85		
July	0.74	0.41	0.82		
October	0.81	0.67	0.90		
January	0.95	0.87	0.95		

Of the seven spring, summer, or fall upwelling-month models found significant by the weighted t-test (Tables 3.6-3.8), only one, July-upwelling at 48°, was among the best-fitting. In spite of this paucity of best-fitting, significant spring-through-fall upwelling-month models, it is nevertheless informative to study the patterns displayed in the t-statistics, particularly at 45° and 48° N latitude. Firstly, at these latitudes, linear-term t-statistics for September- through November-upwelling are all positive. Bakun indices are largely negative for these upwelling months so the interpretation is that stronger downwelling increases survival. Because stronger downwelling occurs during these months when fall transition (transition from upwelling to downwelling) is early (in September), the earlier the transition, the better. Secondly, at 45° and 48°, linear-term tstatistics for June- through August-upwelling are all negative. During the study years, Bakun indices were always positive for these upwelling-months. The interpretation is that increased upwelling improves survival during these months. The fact that the July-upwelling model for 48° identified a bowl-shaped relationship (Figure 3.5, Table 3.11) between survival and upwelling suggests that within this period of enhanced survival, there are periods of better and worse survival that are dictated by upwelling indices. Thirdly, at 45° and 48°, there is a change in direction of linear effects (i.e., change in the sign of linear-term t-statistics) in alternating months from February through June. There appear to be alternating periods of upward and downward survival trend at these latitudes, driven in some way by Bakun upwelling/downwelling effects, with downward swings in survival occurring between February and April, and between April and June.

Among the climate indices fit to Eq. 3.1, one was both significant and best-fitting, the northward upwelling extent during June (JNUE) (Figure 3.7, Table 3.10, 3.11). The covariate JNUE

had a negative effect on survival (p-value =0.04) and significant concave down curvature (p-value =.05) (Figure 3.7), indicating optimal survival at a point near the low extreme of the range of this index. For example, when upwelling conditions do not extend far north in June, or equivalently, when downwelling conditions prevail as far south as 48°N, in June, survival is better. It may be that these are the conditions that also prevail when fall transition is early and winter downwelling is strong.

Figure 3.7: Fitted curves to Eq. (3.1) of first-year survival,  $S_1$ , against June Northward Upwelling Extent (JNUE). Equations evaluated at the mean value for weight-at-release, Wt.

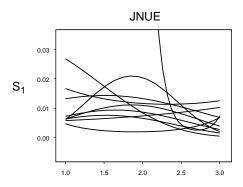


Table 3.10: Results of across-hatchery tests of effect for five annual climatic indices, Pacific Northwest Index (PNI), North Pacific Index (NPI), June Northward Upwelling Extent (JNUE), cumulative May-September Bakun indices at  $45^{\circ}$  and  $48^{\circ}$  N latitude. Lightly shaded cells indicate significance at  $\alpha=0.10$ , dark shaded cells significance at  $\alpha=0.05$ .

		es			
Ocean Covariate	Linear		Quadratic		Number Hatcheries
	t-statistic	p-value	t-statistic	p-value	ŹĤ
PNI	0.78	0.46	2.65	0.03	10
NPI	1.35	0.21	0.51	0.62	9
JNUE	2.42	0.04	2.3	0.05	10
CUM45	-0.4	0.7	1.55	0.16	10
CUM48	-1.29	0.23	0.27	0.79	9

Table 3.11: List of ocean covariates meeting final selection criteria of consistent effect (significant t-test, Eq. 2.9) and goodness-of-fit (2.13). These covariates (column 1) have significant effects on first ocean-year survival. Column 2 shows direction of each significant effect, one direction symbol for covariates having one significant effect and two symbols for covariates with both linear and quadratic terms significant. Downward pointing arrows ( $\downarrow$ ) denote significant negative linear trend with survival (inverse relationship). Upward pointing arrows ( $\uparrow$ ) denote the covariate had a positive linear effect on survival. Significant concave downward quadratic effects, denoted  $\cap$ , had maximum survival in the middle of their range. Significant concave upward quadratic effects, denoted  $\cup$ , had minimum survival in the middle of their range. Column 3 displays the level of significance ( $\alpha = 0.05$  or  $\alpha = 0.10$ ) associated with each effect schematized in Column 2.

Ocean Covariate	Covariate's Linear and Curvilinear Effect Direction(s)	Significance Level(s) of Effect(s)
November SST	<b>+</b>	.10
December SST	<b>↓</b>	.05
July upwelling at 48° N	U	.10
JNUE	<b>↓</b> N	.05,.05
April SST	<b>↓</b>	.05
December upwelling at 48° N	<b>↓</b>	.05
December upwelling at 42° N	<b>↓</b>	.05
June SST	<b>+</b>	.05
January upwelling at 45° N	<b>↑</b> U	.10,.05

#### **Correlations**

Strong correlations between SST-months (which were all positive), generally tended to be between months that were adjacent, such as January/February, February/March, and so on. The only strong (r>0.6) correlations between non-adjacent SST-months were between April and June SST, April and November SST, and April and December SST.

The strongest correlations (r>0.4) between upwelling-months (all were positive) at 42°N (i.e., January/February, January/June, February/March, February/November, March/July, March/November, and September/December) were, in general, not as strong as those between SST months, and were more frequently between non-adjacent months than between adjacent months.

There was a noteworthy pattern among the strong correlations between SST-months and upwelling-months at  $42^{\circ}$  (all were negative). Every strong correlation (|r| > 0.6) with an upwelling-month was with a same-month or subsequent-month SST-month (Table 3.12). There was a cluster of strong correlations early in the year, that is, with January, February, and March upwelling. A second cluster of moderately strong correlations appears to be associated with March and April upwelling. There were strong and moderately strong negative correlations between January-upwelling at  $42^{\circ}$  and June SST, and between January-upwelling and April SST.

Table 3.12: Correlations between SST-Months and Upwelling Months at 42°N latitude.

SST- months	Upwelling-Months											
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Jan	-0.6	-0.45	-0.39	-0.12	-0.25	-0.58	-0.02	-0.09	-0.19	-0.53	-0.47	0.11
Feb	-0.7	-0.54	-0.21	0.14	-0.05	-0.29	0.31	0.27	0.15	-0.11	-0.29	0.06
Mar	-0.7	-0.65	-0.20	0.10	-0.24	-0.32	0.22	0.26	0.05	-0.14	-0.38	-0.12
Apr	-0.5	-0.51	-0.61	-0.19	-0.29	-0.48	-0.07	0.09	0.13	-0.12	-0.29	0.06
May	-0.2	-0.36	-0.35	-0.11	-0.23	-0.39	-0.18	0.27	-0.2	-0.22	-0.36	0.03
Jun	-0.6	-0.30	-0.41	-0.44	-0.36	-0.48	0.13	-0.07	-0.1	0.14	0.13	0.15
Jul	-0.1	-0.23	-0.50	-0.51	-0.23	-0.34	-0.53	-0.12	-0.08	-0.01	0.08	0.08
Aug	0.1	0.03	-0.51	-0.50	-0.27	-0.37	-0.22	-0.57	0.09	-0.10	-0.15	0.27
Sep	0.1	0.08	-0.15	-0.46	-0.07	-0.12	-0.14	-0.51	-0.23	-0.04	-0.06	0.03
Oct	-0.3	-0.23	-0.20	-0.51	-0.39	-0.26	0.06	-0.19	-0.29	-0.25	-0.21	-0.09
Nov	-0.2	-0.40	-0.20	-0.43	-0.10	-0.21	-0.14	0.07	-0.03	-0.35	-0.42	-0.09
Dec	-0.3	-0.33	-0.17	-0.32	0.04	-0.20	-0.19	0.13	-0.03	-0.27	-0.39	-0.17

There was a very strong (r>0.7) correlation between January upwelling at  $42^{\circ}N$  and NPI. There were no other strong correlations between NPI and upwelling-months. There were three very strong negative correlations (r < -0.7) between NPI and SST during the months of January, February, and March.

It is striking that the only strong correlations between non-adjacent SST-months are between those SST-months singled out by the model-selection criteria as significantly affecting survival. The strong correlations between these months suggest that one underlying phenomenon appears

to be the cause of all four significant relationships. That is, there are not four different processes but one common process behind the SST model results.

The lack of strong correlations between adjacent upwelling-months at 42° N latitude suggests that, unlike SST, abrupt and irregular changes through time are the norm for the Bakun index. Two correlations between upwelling-months which invite speculation are those between January and June and between September and December. They may imply that early spring transition, in January, is followed by good upwelling conditions in June, and that early fall transition, in September, is followed by good downwelling conditions in December.

Correlations between upwelling and SST suggest that temperature (measured between 45° and 48° N latitude, Figure 1.1) is driven by upwelling conditions at 42°N latitude, early in the year. The cluster of strong correlations early in the year suggest that, in particular, January-SST is driven by January-upwelling, and February- through April-SSTs are driven by January/February upwelling. The fact that April-SST and June-SST moderately to highly correlated with January upwelling, but May-SST is only weakly correlated with January-upwelling is suggestive of the same puzzling reversal of trend observed in the February through June model results at 45° and 48° N latitude. A second cluster of moderately strong correlations are associated with March- and April-upwelling. The two clusters of correlations, one associated with January/February, the other associated with March/April, may in some way reflect the dual effects noted in January, or, more generally the way SST responds to spring transition.

The strong correlations between January-upwelling and the North Pacific Index (NPI), and between January-, Febuary- and March-SST and NPI serve to underline the prominence of January upwelling (which "drives" January through March SST). The covariate NPI was not a significant index of survival, but it is worth recalling that it is an indicator of the strength of the Aleutian Low pressure system. High (positive) values of NPI (indicating higher pressure, i.e., weaker, less intense) fronts are conditions associated with stronger upwelling in the California Current, conditions that are favorable for West Coast stocks.

## 4.0 Discussion

#### Hatchery Management Implications

Considerable resources and time have gone into investigating the deleterious effects of supplementation on the viability of salmon stocks over the last two decades (NOAA, 1998). Yet, astonishingly, a 1998 NMFS technical memorandum on hatchery regulation reported that no one agency was in charge of hatchery practices in the Columbia Basin and, in fact, "[n]o one is asking the fundamental questions of which hatcheries are doing well and which are doing poorly" (Flagg and Nash, 1999). This current study and others like it (e.g., Anderson and Hinrichsen 1996) supplies timely and crucial information for use by new hatchery monitoring and evaluation initiatives, concerning hatchery release practices. The effect of size at release was found highly significant, six of 10 hatcheries showing significant positive effect on survival with increasing weight, in the first-order model (all p-values < 0.003), and the overall, across-hatchery effect also highly significant (p-value = 0.02).

Although release-month was not tested using the MPH model in this study, a pilot study was performed to investigate the relative importance of "by-entry" versus "by-month" SST/upwelling covariates in accounting for variability in adult return rates. The distinction between these two types of covariates now follows. In the pilot study, release batches were used as replicates rather than brood years. This is important because each brood-year replicate may consist of several batches of fish, each released during a different month and this is a modeling strategy which may be exploring ocean-entry conditions for some fish but not for others. Using batches as replicates allows survival for each batch to be modeled against conditions timed to actual entry, thus "byentry" covariates. The pilot study defined "by-entry" covariates as SST/upwelling measurements taken during the release month, and during the first, second, and third months after release. These by-entry covariates were distinguished from SST/upwelling conditions for January, February, and so one, i.e., "by-month" covariates. The pilot study revealed that "by-entry" covariates accounted for variability in hatchery adult returns more frequently than "by-month" covariates did (chisquare > 30, p-value << 0.001). The pilot study also found that release-month itself, treated as a factor was significant more often than expected (chi-square = 9.00, p-value = 0.003). Fish that are released at different times are subject to different ocean conditions, but in addition they are sub-

ject to different transitional risks. For example, chinook salmon fry released near the mouth of the Columbia River before the plume has formed are thought to have a much higher risk of mortality than fish who enter the low-salinity, nutrient-rich, transitional habitat of a well-formed plume (Anderson and Heinrich 1999, Brodeur and Peterson 1997, Welch 1997). To take another example, the pulsed character of prey and competitor abundance observed in estuarine habitat would make mortality highly dependent on time of entry, which depends on time of release. Interactions between release location and release time are likely to be important.

#### Ocean Effects

Welch (1997) asserted that SST is the most important determiner of ocean distribution for Northeast Pacific salmon species. His research shows the existence of sharp thermal limits, which vary from month to month, for all species. This view interprets monthly ocean distributions as portions of a stock's annual bioenergetic map of survival. The results of this study lend support to Welch's ideas insofar as SST was by far the most consistent of the monthly covariates in its effect on the survival, showing negative influence during 11 out of 12 months. Temperature affected survival more profoundly during April, June, November and December than it did during other months. Nickelson (1986) and Ryding and Skalski (1999) found June SST significant for coho salmon survival. Hyun (1996) found winter SST off the Canadian coast more significant for fall chinook salmon survival than SST during other seasons. Why temperature is more important during some months than others is not clear. One notion that emphasizes the significance of winter SST is that wintertime temperature "preconditioning" (Loggerwell, 2000) of fry and smolts is important to subsequent survival (Dickoff, 1989). Match/mismatch hypotheses, such as might identify particular time periods as limited and crucial windows of, say, foraging opportunity (e.g. Anderson and Hinrichsen, 1996), would appear unlikely explanations here, in view of the high correlation between significant SST-months, which suggest one underlying phenomenon, rather than two or more local ones.

Model results on upwelling indices essentially are of two types, each manifesting a particular kind of coherence. On the one hand are significant effects associated with wintertime downwelling/upwelling, in December and January in particular, which appear at all latitudes studied. The strong role played by January-upwelling in various pairwise correlations and in model results

suggest that January is the locus of important effects, which continue to play out over the ensuing months. Fall subyearling chinook salmon juveniles survive their first ocean-year better during years when either downwelling is strong in January (around -250 units) or transitional conditions (approximately 0 Bakun units) exist in January. Conversely survival is poorest during years when downwelling in January (and December) is weak (e.g. at approximately -180 to -80 units at 45°N). The results suggest that spring transition date is an important indicator of survival, although it was not tested in this study. It was found important by several investigators (Ryding and Skalski 1999, Hyun 1996, Anderson and Heinrich 1999).

The second category of coherent model results on upwelling-months is the appearance of seasonal effects found during spring, summer, and fall at the two northerly latitudes, 45° and 48°N. These trends are important because all the hatchery stocks in this study are believed to move northward after entry into the ocean (Healey, 1991), including the southern-most Elk River Hatchery stock (NOAA, 1998). Increased summertime upwelling, believed to indicate better foraging conditions because of enhanced food availability and lower bioenergetic (temperature) risks, improved survival. Early fall transition, i.e., strong downwelling during fall had a favorable effect on survival, a result also observed for Columbia River spring chinook (Anderson and Heinrich, 1999). The conundrum of alternating months showing opposite survival trend in spring may be the manifestation of the mixing of two or more waves, originating in the dual effect in January, and propagating through time. The bowl-shaped effect described by the July-upwelling at 48° model may reflect the observation (Healey, 1991) that catches of juvenile chinook decline during peak temperatures in July and increase again with cooling temperatures in August and September.

The inverse relationship between survival and JNUE, a measure of upwelling strength, is consistent with concave down curvature in June at 48° (Table 3.7). These results support speculation that upwelling which is too intense may be harmful and that pulsed or variable upwelling creates more favorable conditions than continuous strong upwelling (Loggerwell 2000, Brodeur and Peterson, 1997). The effects of variability in upwelling were not investigated in this study.

#### Additional Comments

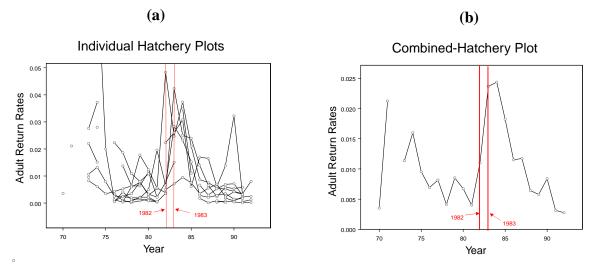
There may be particular value in regional studies such as this one. Evidence suggests individual hatchery stocks have unique ocean distributions (Welch 1997, Hyun 1996), implying that local-scale studies can have large importance for individual ESUs. For example, Coronado-Hernandez (1995) did not find weight at release to have significant effect on adult return rates of CWT fall chinook salmon reared in hatcheries in California, Idaho, Oregon, Washington, Alaska, and British Columbia, in an analysis seeking global effects on the combined data from hundreds of hatcheries. However, in this study of 10 hatcheries, six showed significance (p-value < 0.10). If ocean distributions are highly unique to individual stocks, regional studies are indeed more likely to pick up important local trends. In addition it is hoped this study helps to encourage further interest in studies analyzing CWT release and recovery data which comprises "a wealth" (Healey, 1991) of historical information, still largely unmined.

The MPH model of Ryding and Skalski (1999) coupled with the utilization of CWT hatchery release and recovery data was able to identify several effects which were both useful and consistent with previous findings, with biological expectations, or both. The success of this study should be an inducement to use this modeling approach to analyze other salmon data sets for climatic effects on first ocean-year survival, particularly in view of its having overcome several potential obstacles. One potential obstacle that appears to be general to the approach is the multi-year gaps and high variability in the CWT survival data. The MPH model may present advantages for use with such data insofar as catch effort is not required to be estimated, thus dispensing with an additional layer of uncertainty. A difficulty that is likely to be specific to fall chinook salmon is the small size of ocean-going migrants, which makes the transition between freshwater and marine habitats particularly difficult to understand because of their long rearing periods in estuaries, protected coastal waters, and river plumes.

Finally, although not tested statistically, increased adult returns of CWT fall chinook salmon from 1982-1983 brood years were observed graphically (Figure 4.1). These years were strong El Nino years and similar observations were reported by Hyun (1996) and Mahnken, et al. (1998) of CWT marked fall chinook salmon stocks in the Northeast Pacific ocean. The observation distinguishes fall chinook stocks from those of other *Oncorynchus* species which were adversely

affected by El Nino. Note that the adult returns recorded for 1982 and 1983 in Figure 4.1 were total returns by brood year. That is, smolts from brood year 1982 first entered the ocean in 1983, and brood year 1983 smolts first entered the ocean in 1984, both entry years being peak survival years, as displayed in the combined data (Figure 4.1.b).

Figure 4.1: Plots (with data gaps) of adult return rates by year for (a) all hatcheries and (b) combined hatchery data, showing higher adult return around El Nino years 1982-1983.



# 5.0 Conclusions

The important findings of this study were

- There was a significant positive effect of weight-at-release on the survival of first ocean-year fall chinook salmon raised in hatcheries included in this study.
- Timing of release (release month) was explored graphically and was found to have a positive effect on survival through the month of September. Release month effect was explored in a pilot study using a generalized linear model and was found to have a significant effect.
- The ten hatcheries had unique age-at-return and strongest year-class characteristics which were highly consistent from year to year.
- A preliminary study into the effects of aggregating tagcode batches showed no difference between aggregated and unaggregated data with respect to model selection.
- There was a negative effect of SST on first ocean-year survival for every SST-month except January. The significant SST-months were April, June, November, and December. Strong pairwise correlations between April/June, April/November, and April/December suggest there is one process underlying the effects, rather than four.
- There was significant positive effect of increasing December downwelling on survival.
- There was a significant positive effect on survival when transitional conditions (early spring transition) occurred in January. Strong downwelling in January was also favorable, but not as favorable as transitional downwelling-to-upwelling conditions. Weak downwelling in January was unfavorable for survival.
- There was a significant concave upward curvature for July-upwelling at 48°N latitude. That is, upwelling at the low and high ends of the range of Bakun indices recorded during July between 1970 and 1992 affected survival positively, the higher upwelling more favorable. Decreased survival was associated with Bakun indices in the middle of the range of indices recorded during July at 48°N latitude.
- There was a significant negative effect of the annual June Northward Upwelling Extent (JNUE). JNUE is a measure of the northward extent of upwelling during the month of June. That is, too intense upwelling was unfavorable for survival.
- At 45 and 48 degrees latitude, three distinct trends were observed in the MPH model results. 1) all fall months (September-November) showed increased survival with stronger downwelling, i.e., earlier fall transition improved survival), 2) all summer months (June-August) showed increased survival with increased upwelling, 3) spring months (March-May) showed alternating effect, by month, with March and May Bakun indices showing negative effect on survival and April showing positive effect.
- Bakun indices showed higher inter-latitude correlation during January and December, and lower inter-latitude correlations during July and August, explaining why January and December upwelling effects appeared consistent across latitudes, while July and August upwelling effects change from latitude to latitude.
- January upwelling was found, uniquely, to possess strong pairwise correlations with other
  important covariates, including April and June SST and NPI (an annual measure of the
  strength of the Aleutian Low pressure front). A cluster of strong correlations between
  upwelling-months and same- or subsequent-month SST-months during the beginning of the
  year, that is, between January-upwelling and January- or subsequent SST-months, between

February-upwelling and February- or subsequent SST-months, and between March-upwelling and March or subsequent SST-months.

SST had a negative effect on first ocean-year survival of these fish, particularly in April, June, November, and December. The high correlations between these significant SST-months suggest their biological importance can be traced to one underlying process, rather than two or more, and this discounts the plausibility of match/mismatch explanations. At the northerly latitudes where all the stocks in this study migrate after entering the ocean, increased upwelling had a positive effect on survival during summer months (June-August), with a significant bowl-shaped effect found for July. At these latitudes, increased downwelling during the fall months (September-November) had a positive effect on survival, that is, early fall transitions are more favorable than late. Increased downwelling during December also had a positive effect on survival, and this effect was significant. Finally, two distinct scenarios during January improved survival, strong downwelling and transitional conditions (from downwelling to upwelling or spring transition). During years when downwelling was weak in January, survival decreased. Of the two scenarios that improved survival, transitional conditions were best and this effect was significant. The dual effects in January may play out in complex ways to explain alternating survival trends with increased upwelling in April having positive effect on survival, and increased upwelling in March and May having negative effects on survival.

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Table A1: Coded-wire tag (CWT) releases and returns data by brood year for Abernathy Hatchery.

Brood	Releases			Ret	urns			Non-
Year		Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	recoveries
73	199465	609	908	141	21	32	0	201176
74	239215	330	1060	89	26	0	0	240720
75	65276	17	176	31	0	0	0	65500
76	141964	97	475	37	0	0	0	142573
77	429870	552	1623	107	0	0	0	432152
78	111676	88	531	91	0	0	0	112386
79	150264	170	717	73	2	0	0	151226
80	81676	247	673	31	0	0	0	82627
81	111161	38	171	42	0	0	0	111412
89	44002	6	74	1	0	0	0	44083
90	45264	4	25	6	0	0	0	45299
91	258839	70	461	52	3	0	0	259425
92	292645	163	527	24	0	0	0	293359

Table A2: Coded-wire tag (CWT) releases and returns data by brood year for Big Creek Hatchery.

Brood	Releases			Ret	turns			Non-	
Year		Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	recover- ies	
71	41915	0	316	465	122	7	0	42825	
76	284509	22	137	39	0	0	0	284707	
77	211106	43	392	85	2	3	0	211631	
78	224083	48	481	231	16	0	0	224859	
79	284944	182	1663	399	2	0	0	287190	
80	146845	28	332	71	2	0	0	147278	
81	130541	21	474	188	10	0	0	131234	
82	93069	196	3181	1339	11	0	0	97796	
83	111668	40	1214	1443	127	0	0	114492	
84	95160	94	952	2482	161	1	0	98850	
85	142475	106	1722	1181	54	6	0	145544	
86	462040	277	2193	1528	52	0	0	466090	
87	458099	275	1996	1184	41	0	0	461595	
88	468751	167	1529	881	22	0	0	471350	
89	311377	98	869	628	21	0	0	312993	
90	307022	126	640	507	63	0	0	308358	
91	314734	79	485	515	5	0	0	315818	
92	208529	102	929	618	38	0	0	210216	

Table A3: Coded-wire tag (CWT) releases and returns data by brood year for Elk River Hatchery.

Brood	Releases			Re	turns			Non-	
Year		Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	recover- ies	
73	75547	62	947	1024	110	0	0	77690	
74	143874	49	2299	2863	337	17	0	149439	
77	52781	12	250	447	25	0	0	53515	
78	54123	3	178	160	8	3	0	54475	
79	156231	34	1543	1001	207	36	0	159052	
80	113386	130	541	596	141	11	3	114808	
81	191113	81	282	595	102	13	1	192187	
82	134648	33	252	207	27	3	0	135170	
83	101435	343	1549	1998	547	51	5	105928	
84	261509	355	2418	2844	970	127	20	268243	
85	308982	489	2950	3368	616	164	7	316576	
86	216659	119	856	1956	113	4	0	219707	
87	99122	41	385	192	24	12	0	99776	
88	184075	53	192	134	41	10	0	184505	
89	103680	76	189	253	78	13	1	104290	
90	339356	194	303	829	390	108	6	341186	
91	295040	98	376	891	304	62	6	296777	
92	333393	379	1318	1964	716	91	0	337861	

Table A4: Coded-wire tag (CWT) releases and returns data by brood year for Elokoman Hatchery.

Brood	Releases			Ret	urns			Non-	
Year		Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	recover- ies	
73	83264	15	313	352	122	6	0	84072	
76	144564	19	271	177	13	0	0	145044	
77	147829	35	34	72	8	0	0	147978	
78	138929	3	19	4	4	0	0	138959	
79	98334	1	35	41	1	0	0	98412	
80	165381	1	103	128	24	10	0	165647	
81	102754	0	17	22	1	0	0	102794	
85	194494	150	911	354	50	1	0	195960	
88	229325	6	69	58	0	0	0	229458	
91	89391	0	26	18	0	0	0	89435	
92	182291	0	76	128	27	0	0	182522	

Table A5: Coded-wire tag (CWT) releases and returns data by brood year for Grays River Hatchery.

Brood	Releases			Ret	turns			Non-	
Year		Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	recover- ies	
74	4708	1	428	213	17	0	0	5367	
75	36119	31	405	272	28	0	0	36855	
76	150805	0	86	85	2	0	0	150978	
77	143125	12	36	6	3	0	0	143182	
78	241811	1	73	80	15	0	0	241980	
79	37374	0	38	34	10	0	0	37456	
80	74116	4	29	100	27	0	0	74276	
81	72788	2	20	11	0	0	0	72821	
82	96791	7	97	230	10	0	0	97135	
84	198367	315	1305	4334	1196	84	3	205604	
85	362511	234	1278	2042	469	6	0	366540	
88	98509	0	29	3	0	0	0	98541	
89	266514	13	44	124	9	0	0	266704	
90	262490	9	36	43	15	0	0	262593	
91	266642	4	10	8	0	0	0	266664	
92	337401	0	16	48	6	0	0	337471	

 $\label{thm:coded-wire tag} \textbf{(CWT)} \ \textbf{releases} \ \textbf{and} \ \textbf{returns} \ \textbf{data} \ \textbf{by} \ \textbf{brood} \ \textbf{year} \ \textbf{for} \ \textbf{Klaskanine} \\ \textbf{Hatchery.}$ 

Brood	Releases			Ret	urns			Non-	
Year		Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	recover- ies	
74	62922	13	699	1101	419	16	0	65170	
76	95579	0	41	5	2	0	0	95627	
77	100618	58	297	59	0	0	0	101032	
78	243758	11	187	119	1	0	0	244076	
79	66228	9	74	20	0	0	0	66331	
80	100929	3	72	4	0	0	0	101008	
81	100217	0	35	12	0	0	0	100264	
86	194311	23	218	105	0	0	0	194657	
87	203526	0	12	8	0	0	0	203546	
88	209011	28	119	29	0	0	0	209187	
89	108296	0	12	13	0	0	0	108321	

Table A7: Coded-wire tag (CWT) releases and returns data by brood year for Quinault Lake Hatchery.

Brood	Releases			Ret	urns			Non-	
Year		Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	recover- ies	
77	235716	12	16	39	25	0	0	235808	
78	198049	30	324	673	151	11	0	199238	
79	33735	6	57	141	48	8	0	33995	
80	98023	14	73	134	98	6	3	98351	
81	167692	9	74	177	83	25	0	168060	
82	140863	14	188	375	417	100	3	141960	
83	164037	11	230	1261	897	114	0	166550	
86	99260	1	32	89	399	140	4	99925	
87	151248	1	33	132	231	50	6	151701	
88	147159	10	97	270	363	37	0	147936	
89	142139	2	142	329	465	51	1	143129	
90	136115	3	145	366	396	69	0	137094	
91	92539	0	40	60	157	10	0	92806	
92	93895	0	7	91	129	8	0	94130	

Table A8: Coded-wire tag (CWT) releases and returns data by brood year for Quinault National Fish Hatchery.

Brood	Releases			Ret	urns			Non-	
Year		Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	recover- ies	
73	168372	38	543	1091	135	4	0	170183	
74	90186	17	354	512	310	20	0	91399	
75	93107	19	253	380	86	0	0	93845	
76	192768	13	171	251	56	0	0	193259	
77	93138	10	83	91	41	0	0	93363	
78	94938	4	38	115	26	2	0	95123	
79	91599	8	33	98	34	0	0	91772	
80	142342	46	165	403	90	0	0	143046	
81	27006	13	59	353	106	8	0	27545	
82	93125	8	109	270	223	12	3	93750	
83	45066	59	381	631	224	20	3	46384	
84	50734	30	313	477	361	28	0	51943	
85	198147	20	451	1222	1124	241	4	201209	
86	199434	6	87	250	213	12	4	200006	
87	192986	3	26	149	188	43	0	193395	
88	160666	2	55	208	176	11	0	161118	
89	186736	6	68	233	347	9	3	187402	
90	192955	3	16	123	103	35	0	193235	
91	157821	0	42	71	138	7	0	158079	
92	353667	2	112	482	450	32	0	354745	

 $\label{thm:coded-wire tag} \textbf{ (CWT) releases and returns data by brood year for Salmon River \\ \textbf{ Hatchery.}$ 

Brood	Releases			Ret	turns			Non-	
Year		Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	recover- ies	
76	47026	79	314	446	230	6	0	48101	
77	42957	269	252	228	67	1	0	43774	
78	41207	50	161	173	68	1	0	41660	
79	48749	17	81	115	165	16	0	49143	
80	53098	35	120	182	223	19	3	53680	
82	25160	15	63	214	256	26	0	25734	
83	25470	35	117	216	282	30	0	26150	
84	46347	160	224	655	403	29	0	47818	
85	50510	21	38	87	136	28	0	50820	
86	135750	183	241	738	1048	130	6	138096	
87	190273	383	487	1086	1187	50	3	193469	
88	171312	97	126	498	299	24	0	172356	
89	200554	162	553	841	1175	76	1	203362	
90	178180	444	1037	2445	1920	83	0	184109	
91	184316	37	144	218	186	8	3	184912	
92	166687	255	912	773	715	11	0	169353	

Table A10: Coded-wire tag (CWT) releases and returns data by brood year for Trask Hatchery.

Brood	Releases			Ret	urns			Non-
Year		Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	recover- ies
70	51204	0	60	15	100	6	0	51385
73	73741	124	865	479	193	0	0	75402
74	37655	7	198	250	116	7	0	38233
82	140075	18	127	382	148	26	0	140776
83	139876	45	214	331	377	30	0	140873
84	137803	11	95	421	624	167	0	139121
85	82420	3	36	150	371	64	3	83047
86	141916	15	53	201	191	30	2	142408
87	85849	4	71	182	203	17	0	86326
88	66664	10	59	258	118	25	0	67134
89	50707	0	17	46	50	2	0	50822
90	44576	0	11	97	66	12	0	44762
91	38731	3	6	46	68	1	0	38855
92	51389	1	51	234	84	2	0	51761

Table B1: Bakun upwelling indices for 1970-1994 for 42,45,48,51, and 54 degrees N. latitude

o N lat	Yr	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
42	1970	-156	-62	18	98	110	98	154	160	71	0	-48	-72
42	1971	-1	13	-23	26	145	75	119	52	30	23	-9	-8
42	1972	-4	-64	-3	29	101	155	119	95	44	60	-34	-43
42	1973	-89	-53	32	125	106	125	186	198	19	6	-41	-116
42	1974	-8	-17	-16	31	152	177	87	135	38	41	-22	-23
42	1975	-11	-65	6	89	101	220	133	123	72	-11	-17	-12
42	1976	-10	-4	20	15	132	166	95	44	52	7	-23	-27
42	1977	-21	-57	44	27	36	203	192	79	32	4	-18	-110
42	1978	-170	-68	0	10	111	87	192	73	8	33	4	3
42	1979	-30	-69	3	13	100	153	62	46	8	-4	-88	-146
42	1980	-7	-124	22	6	122	83	152	179	29	-3	-46	-116
42	1981	-179	-39	-1	44	66	78	201	78	15	-1	-69	-105
42	1982	-7	-31	-2	3	189	66	97	51	37	-22	-49	-97
42	1983	-212	-256	-129	8	56	77	61	43	61	0	-144	-22
42	1984	-17	-85	-9	18	21	101	181	63	31	-4	-117	-4
42	1985	-32	9	5	21	32	89	80	63	21	1	1	-80
42	1986	-269	-72	-19	47	14	35	118	77	11	-6	-1	-101
42	1987	-90	-12	-26	13	55	81	66	140	38	9	-40	-38
42	1988	-92	0	11	6	13	65	136	122	44	4	-56	-4
42	1989	0	-1	-43	5	66	78	128	109	27	2	0	-16
42	1990	-23	-9	1	30	26	46	122	45	46	12	0	2
42	1991	-21	-45	10	40	135	169	171	49	77	33	-5	-28
42	1992	-118	-123	3	-2	141	99	126	117	42	0	-11	-21
42	1993	-39	-36	-18	-23	-1	86	185	126	72	5	6	-75
42	1994	-40	-31	0	32	75	98	195	93	36	21	-10	-100
45	1970	-98	-71	1	25	33	46	71	73	11	-7	-54	-106
45	1971	-32	-16	-49	-2	66	13	65	24	8	1	-40	-27

Table B1: Bakun upwelling indices for 1970-1994 for 42,45,48,51, and 54 degrees N. latitude

o N lat	Yr	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
45	1972	-19	-103	-25	-1	34	55	52	56	19	34	-64	-68
45	1973	-111	-43	-1	43	25	27	76	103	3	-3	-46	-129
45	1974	-36	-51	-37	2	26	80	36	72	16	6	-46	-75
45	1975	-33	-77	-1	35	26	98	68	40	38	-48	-79	-44
45	1976	-41	-30	-10	0	21	56	23	17	14	0	-31	-47
45	1977	-40	-109	8	1	9	71	73	41	7	-7	-67	-100
45	1978	-145	-88	-1	-1	28	34	92	13	-5	5	-4	-4
45	1979	-67	-103	0	6	34	86	30	31	0	-8	-127	-157
45	1980	-19	-155	1	-7	52	32	103	96	9	-19	-121	-113
45	1981	-206	-68	-14	0	12	8	107	40	-1	-5	-103	-106
45	1982	-31	-72	-5	-2	79	59	51	38	12	-40	-52	-98
45	1983	-202	-216	-95	3	35	19	18	35	25	-1	-166	-52
45	1984	-29	-131	-33	-8	-2	37	121	37	3	-21	-138	-14
45	1985	-63	-2	-5	5	15	52	83	46	12	-9	-3	-122
45	1986	-301	-55	-36	13	1	25	66	84	10	-7	-16	-149
45	1987	-147	-35	-38	-1	23	43	35	99	17	4	-90	-70
45	1988	-125	-6	-9	0	-6	14	66	71	17	0	-92	-20
45	1989	-16	-15	-59	1	26	43	48	62	28	-1	-12	-22
45	1990	-47	-26	-4	11	9	15	103	25	34	-5	-38	-9
45	1991	-34	-81	1	7	51	59	80	26	58	14	-50	-56
45	1992	-170	-128	4	-11	66	61	81	66	13	-4	-42	-33
45	1993	-55	-50	-35	-64	-4	24	65	65	41	1	-3	-97
45	1994	-44	-50	-7	4	22	28	118	37	17	1	-36	-149
48	1970	-91	-73	-2	23	18	33	43	36	1	-25	-63	-106
48	1971	-26	-18	-55	-14	42	6	39	15	1	-7	-56	-20
48	1972	-8	-83	-32	-5	11	27	15	27	8	5	-84	-66
48	1973	-151	-56	-7	23	9	11	32	54	0	-11	-26	-104
48	1974	-31	-46	-31	-3	12	38	19	37	4	-1	-50	-80

Table B1: Bakun upwelling indices for 1970-1994 for 42,45,48,51, and 54 degrees N. latitude

o N lat	Yr	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
48	1975	-24	-90	-4	17	15	59	45	14	10	-60	-104	-48
48	1976	-63	-35	-24	-3	6	31	5	9	1	-6	-37	-53
48	1977	-45	-99	11	-2	9	39	42	24	2	-30	-65	-63
48	1978	-129	-111	-4	-3	17	28	58	3	-16	0	-16	-10
48	1979	-73	-82	-2	10	24	83	25	35	-2	-16	-187	-140
48	1980	-68	-218	3	-15	41	32	63	68	5	-39	-145	-113
48	1981	-251	-76	-16	-1	8	5	80	24	-6	-10	-123	-102
48	1982	-24	-73	-1	0	59	74	36	38	7	-44	-56	-96
48	1983	-165	-197	-63	5	45	24	18	26	12	-3	-127	-126
48	1984	-42	-143	-29	-14	-1	33	72	27	0	-21	-121	-28
48	1985	-107	-20	-9	7	20	49	79	39	12	-21	-19	-155
48	1986	-327	-69	-52	6	2	26	57	84	9	-17	-25	-194
48	1987	-203	-66	-36	-6	22	37	39	68	9	-1	-102	-115
48	1988	-152	-16	-12	1	-6	12	54	55	15	-5	-90	-44
48	1989	-27	-67	-72	0	34	31	31	48	21	-12	-20	-43
48	1990	-35	-25	-12	7	14	12	61	15	16	-22	-29	-16
48	1991	-45	-82	-1	2	27	31	27	9	17	1	-82	-70
48	1992	-171	-125	0	-8	30	42	52	28	8	-13	-53	-46
48	1993	-102	-82	-39	-55	-2	23	38	26	20	-2	-13	-99
48	1994	-38	-55	-15	-1	7	11	58	10	3	-7	-34	-153
51	1970	-50	-84	-15	36	-12	10	9	8	9	-4	-32	-17
51	1971	-2	-23	-41	-25	11	2	28	-15	10	1	-37	5
51	1972	2	-59	-25	3	2	6	17	4	38	9	-91	-7
51	1973	-75	-50	-3	5	-20	-15	5	40	-6	-19	2	-81
51	1974	5	-37	-6	-9	-3	7	8	44	3	-35	-42	-62
51	1975	-9	-72	2	17	-1	38	6	7	7	-24	-35	-30
51	1976	-81	1	-16	-33	-21	20	-23	4	-12	-6	-68	-48
51	1977	-40	-152	35	-6	9	10	10	27	16	-79	-37	-28

Table B1: Bakun upwelling indices for 1970-1994 for 42,45,48,51, and 54 degrees N. latitude

o N lat	Yr	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
51	1978	-127	-129	-21	-2	6	53	49	-2	-32	-13	-2	21
51	1979	-32	-22	-5	8	-3	15	0	14	-22	-53	-87	-57
51	1980	-12	-110	15	-115	7	24	19	70	17	-81	-77	-40
51	1981	-309	-9	-77	-4	-16	-14	68	3	-43	-1	-86	-45
51	1982	5	-13	0	-4	9	25	8	11	9	-7	-11	-51
51	1983	-191	-156	-43	0	5	-6	0	-1	7	-22	-49	-47
51	1984	-58	-112	-84	-50	-25	-3	7	-2	-18	-32	-41	2
51	1985	-122	4	-5	-4	3	2	13	13	25	-2	0	-108
51	1986	-213	-51	-124	-10	-21	2	20	31	27	-54	-8	-114
51	1987	-89	-43	-13	-70	-4	0	22	40	0	-5	-72	-31
51	1988	-65	-30	-34	-2	-26	-9	3	18	6	-24	-64	-7
51	1989	-1	-11	-50	-1	9	8	0	24	18	-22	-20	-59
51	1990	-8	2	-70	-4	4	1	31	0	5	-19	12	25
51	1991	-32	-93	7	-8	15	20	4	5	3	2	-88	-61
51	1992	-135	-107	-3	-19	7	13	53	11	11	-125	-44	-2
51	1993	-25	-77	-52	-97	-10	4	46	44	57	-9	2	-115
51	1994	-52	-9	-16	-16	-6	1	25	9	-4	-6	39	-63
54	1970	-82	-109	-45	-9	-48	-4	-7	-6	-11	-19	-54	-50
54	1971	-40	-78	-53	-42	-9	0	19	-19	-8	-21	-62	-9
54	1972	-16	-83	-34	-17	-2	-3	3	-12	12	-11	-78	-27
54	1973	-58	-62	-17	-23	-54	-23	-1	9	-15	-74	-5	-141
54	1974	-8	-107	-10	-28	-13	-8	3	17	-13	-137	-111	-129
54	1975	-69	-122	-13	-7	-17	3	-7	-4	-16	-49	-58	-87
54	1976	-159	-18	-40	-55	-55	5	-26	-7	-56	-39	-163	-86
54	1977	-100	-236	-10	-31	0	-9	-9	7	2	-163	-36	-38
54	1978	-145	-163	-51	-5	-24	26	7	-9	-43	-93	-21	-27
54	1979	-63	-48	-27	4	-26	-2	-16	7	-53	-122	-104	-70
54	1980	-51	-131	-26	-190	-2	16	-7	20	-7	-191	-144	-59

Table B1: Bakun upwelling indices for 1970-1994 for 42,45,48,51, and 54 degrees N. latitude

o N lat	Yr	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
54	1981	-370	-21	-105	-11	-24	-12	25	-7	-77	-18	-136	-78
54	1982	-42	-25	-6	-41	-12	11	3	4	-7	-47	-33	-128
54	1983	-256	-176	-57	-1	-10	-5	-4	-22	-6	-60	-66	-64
54	1984	-94	-153	-116	-57	-20	-10	-13	-10	-61	-47	-61	-25
54	1985	-188	-45	-35	-47	-3	-14	7	2	12	-32	-10	-198
54	1986	-305	-107	-132	-50	-34	-3	4	-1	8	-85	-51	-198
54	1987	-137	-91	-26	-159	-45	-46	14	6	-41	-72	-164	-75
54	1988	-78	-116	-104	-24	-35	-28	-14	-5	-25	-69	-121	-51
54	1989	-78	6	-64	-8	1	1	0	7	1	-53	-74	-116
54	1990	-30	-30	-96	-7	4	0	5	-5	-22	-44	-33	-7
54	1991	-47	-123	3	-55	-4	4	-3	-11	-38	-20	-143	-139
54	1992	-219	-106	-14	-24	-5	3	11	-2	-25	-68	-92	-15
54	1993	-23	-76	-84	-80	-2	0	22	16	25	-47	-33	-169
54	1994	-86	-29	-65	-32	-28	-3	2	7	-54	-76	-23	-99

**Table B2: Sea surface temperatures for 1970-1993** 

Yr	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
70	9.08	10.26	10.20	10.23	11.44	12.29	13.17	13.73	12.95	11.90	11.31	10.17
71	8.29	8.55	7.58	9.52	11.36	12.88	14.33	15.84	14.43	12.33	10.16	8.45
72	7.29	8.28	9.31	9.81	11.86	13.13	14.59	14.10	13.18	11.60	10.46	8.97
73	8.52	9.28	9.49	10.09	12.00	12.72	13.33	12.95	13.35	12.48	10.57	9.58
74	7.52	8.65	8.75	9.92	11.09	12.67	14.69	14.24	15.26	12.58	11.28	10.51
75	8.83	8.44	8.67	9.24	11.42	11.84	14.03	13.79	13.74	12.24	10.61	8.87
76	8.19	7.88	7.68	8.97	11.64	12.66	14.15	14.28	14.34	12.97	11.48	9.66
77	8.55	9.27	9.03	9.77	11.22	12.63	13.34	14.13	14.63	14.12	11.90	10.06
78	9.96	9.66	9.51	9.73	11.26	14.84	13.82	13.39	15.21	14.30	11.14	9.76
79	8.40	7.04	8.51	9.96	11.41	12.78	15.43	15.21	16.65	14.72	12.62	10.84
80	9.16	9.18	9.53	9.84	12.27	12.90	15.20	13.82	14.41	13.85	12.66	10.65
81	9.99	10.04	10.40	10.31	12.09	13.86	13.78	15.81	15.27	13.89	11.86	10.48
82	9.51	8.86	8.78	9.87	11.21	11.98	13.57	14.68	14.98	12.74	11.69	10.52
83	10.79	10.56	10.69	11.53	12.43	14.51	15.58	15.86	14.60	14.02	12.43	10.79
84	9.61	9.24	9.70	9.88	11.67	12.20	13.44	15.39	15.05	13.66	11.95	9.80
85	8.48	7.81	8.31	9.12	11.81	12.84	14.87	15.03	13.96	12.14	9.59	9.01
86	9.29	9.33	10.26	10.34	11.34	14.22	15.54	14.36	14.37	13.76	11.30	9.72
87	9.85	9.86	9.81	10.62	12.16	12.99	14.48	14.83	15.15	14.51	13.10	11.18
88	9.58	8.95	9.33	9.92	11.79	13.78	14.65	14.81	14.01	13.87	11.84	10.57
89	8.73	7.48	7.74	10.53	12.18	13.44	15.49	15.90	14.85	13.83	11.75	10.16
90	9.46	8.55	9.15	10.77	11.86	13.40	15.32	16.15	16.54	13.75	11.99	10.05
91	7.61	8.83	8.96	9.91	10.83	12.87	14.05	15.55	15.47	13.47	11.03	10.21
92	9.49	10.27	10.75	10.86	12.21	14.57	15.58	15.30	14.44	13.48	12.80	10.99
93	7.98	8.85	9.37	10.64	11.37	14.89	15.00	15.26	14.86	13.82	11.52	9.70

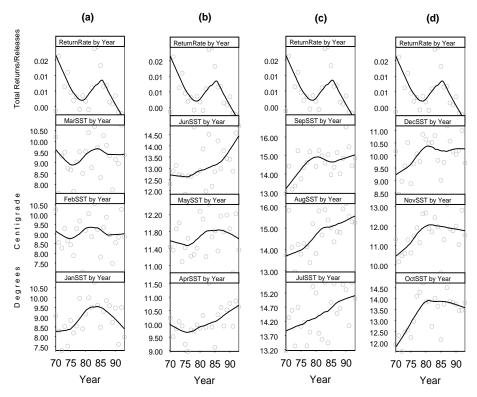
Table B3: Climate and upwelling indices for 1971-1993.

Yr	PNI	NPI	JNUE	cumUpw45	cumUpw48
71	-1.40		2	125	34
72	-1.39	2.45	2	190	51
73	0.33	0.13	1	276	122
74	-1.08	-0.32	3	195	76
75	-0.84	0.64	2	304	156
76	-0.05	0.71	2	121	25
77	0.85	-3.43	2	210	125
78	0.89	-2.89	3	160	83
79	0.43	1.17	2	187	173
80	0.44	-1.70	2	286	197
81	1.16	-4.95	1	152	94
82	-0.25	1.22	3	232	213
83	0.68	-5.92	1	40	67
84	0.52	-3.10	1	155	88
85	0.75	0.62	2	208	197
86	0.33	-4.59	2	163	132
87	1.06	-3.42	1	178	133
88	0.44	-1.25	1	153	119
89	0.35	2.36	3	149	93
90	-1.10	1.52	2	193	113
91	0.11	1.86	3	282	112
92	1.42	-2.93	3	280	152
93	1.03	-0.64	2	92	11

## **Adult Return Trends in Plots against Covariates**

The monthly SSTs against year are plotted in panel strips with combined-hatchery returns in figure C1. The top panel is the same in each strip: combined (across-hatchery) returns (return fractions by brood year). Most notable about the return plot is the trough at around 1980 and the peak at around 1985. The 1980 trough coincides with increasing or peaked temperatures in the monthly SST plots. There is a hint of "in-synch" behavior in the January, March, and May plots.

Figure C1: Monthly sea surface temperatures (SSTs) plotted against years (bottom three panels, all strips) compared with combined (all-hatcheries) return rates plotted against years (top panels, all strips).

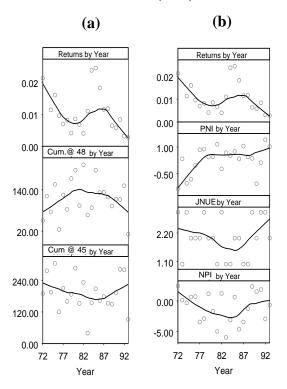


There are pronounced mirror-image relationship between combined returns and temperature in the September and December plots.

Figure C2 shows panel strips of climate indices plotted by year below the combined return rates plotted by year (top panel, both strips). The curves for JNUE, NPI, and cumulative

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Figure C2: (a) Combined (all-hatcheries) return rates plotted (loess-fitted) against year (top panels) compared with cumulative May-September Bakun upwelling indices at 48°N (Cum @ 48) and cumulative May-September Bakun upwelling indices at 45°N (Cum @ 45) against year; (b Combined (all-hatcheries) return rates plotted (loess-fitted) against year (top panels) compared with the Pacific Northwest Index (PNI), June Northern Upwelling Extent (JNUE), and the North Pacific Index (NPI).



upwelling at 45° look similar. There is a hint of "in-synch" matching between PNI and returns curve. The cumulative upwelling index at 48° doesn't appear to correlate well with survival trends for these subyearling fall chinook salmon.

# Adult Return trends by Year by hatchery and combined

Figure C3 shows return fractions by year, for each hatchery. The top panel of each strip is the combined, all-hatchery return rate. Clearly, there is a pattern among many hatcheries of declining return rates from the early 1970's until around 1980, an increase peaking somewhere between 1980 and 1985, and a subsequent decline.

Figure C4 is the raw plot (not loess-fitted) of the data in the top panels in Figure C2.

A problem, made clear in Table C1, is the gaps in the data. Each of the ten hatcheries supplied data from a different set of brood years, resulting in a potential brood year confounding problem. The mean return rates for each year, averaged over hatcheries, is sometimes a single return rate (1970), sometimes an average of two or three hatchery return rates.

Figure C3: (a) Loess-fitted plots of combined (all- hatcheries) return rates against year (top panel) compared with by-hatchery return rates plotted against year for Washington hatcheries Quinault NFH, Quinault Lake, Grays River, Elokoman, and Abernathy (bottom five panels). (b) Loess-fitted plots of combined (all-hatcheries) return rates plotted against year (top panel) compared with by-hatchery return rates plotted against year for Oregon hatcheries Trask, Salmon River, Klaskanine, Elk River and Big Creek (bottom five panels).

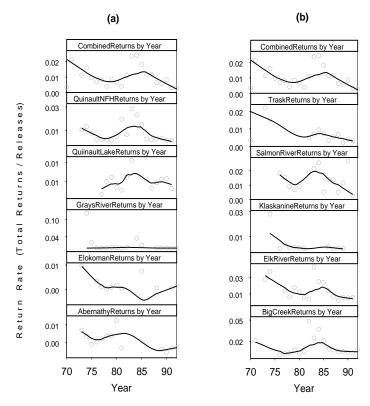


Table C1: Table of return percentages by brood year for each hatchery (table body) and across-hatchery means (bottom row) and across-brood year means (right margin).

					Hatc	heries					
Brood Years	Aber nathy	Big Creek	Elk River	Elok- oman	Grays River	Klas- kanine	Quin- ault Lake	Quin- ault NFH	Salmon River	Trask	Means
70										0.35	0.35
71		2.11									2.11
72											
73	0.82		2.76	0.95				1.06		2.2	1.56
74	0.61		3.72		8.76	2.8		1.33		1.51	3.12
75	0.34				2			0.79			1.04
76	0.43	0.07		0.33	0.11	0.05		0.25	2.23		0.5
77	0.53	0.25	1.37	0.1	0.04	0.41	0.04	0.24	1.87		0.54
78	0.63	0.35	0.65	0.02	0.07	0.13	0.6	0.19	1.09		0.41
79	0.63	0.78	1.77	0.08	0.22	0.16	0.76	0.19	0.8		0.6
80		0.29	1.24	0.15	0.22	0.08	0.33	0.49	1.08		0.48
81	0.23	0.53	0.56	0.04	0.05	0.05	0.22	1.96			0.46
82		4.83	0.39		0.35		0.77	0.66	2.23	0.5	1.39
83		2.47	4.24				1.51	2.84	2.6	0.71	2.4
84		3.73	2.5		3.48			2.33	3.08	0.95	2.68
85		2.1	2.4	0.75	1.1			1.52	0.61	0.75	1.32
86		0.87	1.39			0.18	0.66	0.28	1.69	0.34	0.77
87		0.76	0.66			0.01	0.29	0.21	1.65	0.55	0.59
88		0.55	0.23	0.06	0.03	0.08	0.53	0.28	0.61	0.7	0.34
89	0.18	0.52	0.58		0.07	0.02	0.69	0.35	1.38	0.23	0.45
90	0.08	0.43	0.53		0.04		0.71	0.14	3.22	0.42	0.7
91	0.22	0.34	0.58	0.05	0.01		0.29	0.16	0.32	0.32	0.25
92	0.24	0.8		0.13	0.02						0.3
Means	0.41	1.21	1.5	0.24	1.04	0.36	0.57	0.8	1.63	0.73	0.85

### Rearing Variables and Survival: Weight-at-Release and release-month

### 1. Exploratory generalized linear models analysis

Because of the wide range of release-months, and because of fall subyearling chinook salmon fry are believed to remain in protected coastal waters, river plumes and estuaries for extended rearing periods before venturing offshore, it appeared that any one month was as likely as any other to be the temporal site of important ocean-based effects. A generalized linear model (GLM) analysis was performed which used tagcode release batches as replicates rather that brood-years as replicates. This allowed for the more effective matching of release timing with temperature (SST) and upwelling (Bakun indices) conditions because all fish in a release batch were released within a month of each other, whereas all fish in a brood-year were often release within several months of each other, as brood-years were aggregates of the batches release in a year. In the GLM analysis, "by entry" variables were constructed. They were simply SSTs or Bakun indices during release-month, and during the first, second, and third months after release. SST by-entry variables were named RMO0, RMO1, RMO2, and RMO3, to signify SST during release-month, or one, two, or three months after release-month respectively. Bakun upwelling by-entry variables were named RMO042, ..., RMO342, RMO045, and so on, making sixteen by-entry variable in all. By-month variables were time series (1970-1992) of SST, and Bakun upwelling indices at three latitudes measured during each month, making forty-eight monthly by-month variables in all. For the GLM analysis the Splus function, glm(), was used with a binomial link function and weights equal to release size per batch. I performed GLM analyses for individual hatcheries and for the combined all-hatchery data set. For each hatchery there were 67 variables: 12 SSTmonths, 36 upwelling-months (at 3 latitudes), 12 by-entry variables, average batch weight, broodyear, and release-month. brood-year and release-month variables were treated as factors. I did not look at interactions.

One way to test the significance of a single effect is to compute F-tests for an ANOVA with one effect. Another way is to look at the size of the Cp statistic. Comparing methods for pilot datasets revealed they produce nearly identical results. The Cp statistic was chosen as the variable selection criterion since it is much faster to calculate for single effects in Splus.

For each hatchery the most significant variables, then performed a brief analysis of the select list consisting of identifying strong correlations and finding the combination of effects producing the best model using ANOVA F-tests as criteria.

For the combined-hatchery data set, I also included a hatchery factor variable and a "type" factor variable with 4 levels: Washingon Coastal, Washington Columbia River, Oregon Coastal, and Oregon Columbia River. Howeve, the amount of data (approximately a thousand tagcode batches) made nearly every individual effect significant at the 0.00005 level, with one exception, the "type" which was not significant at the 0.10 level. Although Coronado-Hernandez (1995) found significant effects of region, the region sampled here was probably too small to detect differences.

Table D1 shows the results of the by-hatchery analyses. The most notable conclusions were as follows. 1) Each hatchery analysis identified completely different most significant variables. 2) The by-entry variables were more frequently significant than would be expected from the proportion of variables that were by-entry (31 out of 54 significant SST or upwelling variables were by-entry, while only 12 of the 63 possible variables were by-entry). 3) There was a disproportionately high frequency of identification of weight-at-release or release-month variables. 4) This analysis identified the same most important by-month variables as the multinomial-proportional hazards (MPH) model did, showing the data-aggregation made no difference ranking the relative importance of by-month variables.

Table D1: Results of a generalized linear model analysis to find the most significant variables to explain by-hatchery variability in adult return rates. ByEntrySST means byentry variables (see text) for SST, called RMOi, i=0,...,3 (i.e., RMO0 = SST during the release-month, RMO1 = SST during 1 month after release, ..., RMO3 = SST 3 months after release). ByEntryUpw means by-entry variables (see text) for Bakun upwelling indices, called RMOi42, i=0,...,3 at  $42^{\circ}$  N, RMOi45, i=0,...,3 at  $45^{\circ}$  N, and so on. ByMonthSST variables are time series of SST (1970-1992) recorded during each month, January through December, and ByMonthUpw variables are the upwelling analogs at three latitudes. RMO is release-month treated as a factor, BY is brood-year treated as a factor, WT is average batch weight at release in grams.

Hatchery (# sig. vars)	ByEntryUpw	ByEntrySST	ByMonthUpw	ByMonthSST	Other
Abernathy (6)	RMO042, RMO145° (2)	RMO1 (1)		April (1)	RMO,BY
Bigcreek (11)	RMO242,45,48 RMO342,45,48 RMO148 (7)	RMO2, RMO3 (2)			WT,RMO (2)
Elkriver (7)			May45°, April42°, May48° (3)	December, August, April (3)	BY (1)
Elokoman (6)	RMO045,48 RMO145 (3)	RMO3 (1)	April42° (1)		WT (1)
Klaskanine (7)	RMO148 (1)	RMO2, RMO3 (2)	April42°,45° (2)		WT,RMO (2)
Graysriver (10)	RMO242,45,48 RMO342,45,48 (6)	RMO2, RMO3 (2)		October, November (2)	
Quinlake (4)	RMO045 (1)		May42°, November45° (2)	August (1)	
Quinnfh (3)	RMO042 (1)	RMO2, RMO3 (2)			
Salmriver (3)			October42° (1)	May, July (2)	
Trask (7)			June42°, 45° (2)	August, October, January (3)	BY,RMO (2)
TOTALS:					
64 significant variables	21 ByEntryUPW variables	10 ByEntrySST variables	11 ByMonthUpw variables	12ByMonthSST variables	10 Other
	3 ByEntry		2 ByMonth		
		54 UPW or S	SST variables		

## 2. Data Plots

Because of the importance of by-entry variables in the GLM analysis described in Section 1 of this appendix, exploratory data plots were made of adult return rates against by-entry variables, RMOi, i = 1, ... 8. These plots revealed no simple or clear relationships between return rate and SST.

Examination of the individual weight-at-release and release-month effects was more valuable. Figure D1 shows weight-at-release plotted against returns for each hatchery. Here weight-at-release indices are weighted averages of the batch weights. One striking feature is the lack of uniformity of hatchery practices on this variable. The general trend is of increasing survival with increasing weight, although curvilinear relationships are also present.

Figure D1: Loess-fitted plots of weight at release (in grams) agains total recovery fraction per brood-year, for each hatchery.

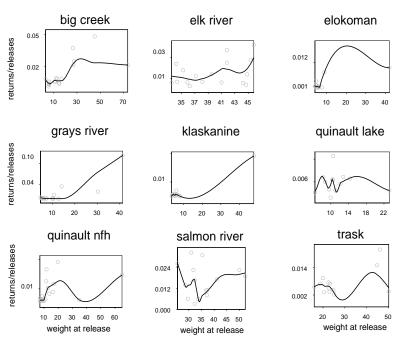


Figure D2: Loess-fitted plots comparing returns by year with weight at release by year for Elk River, Salmon River, Trask, and Big Creek hatcheries.

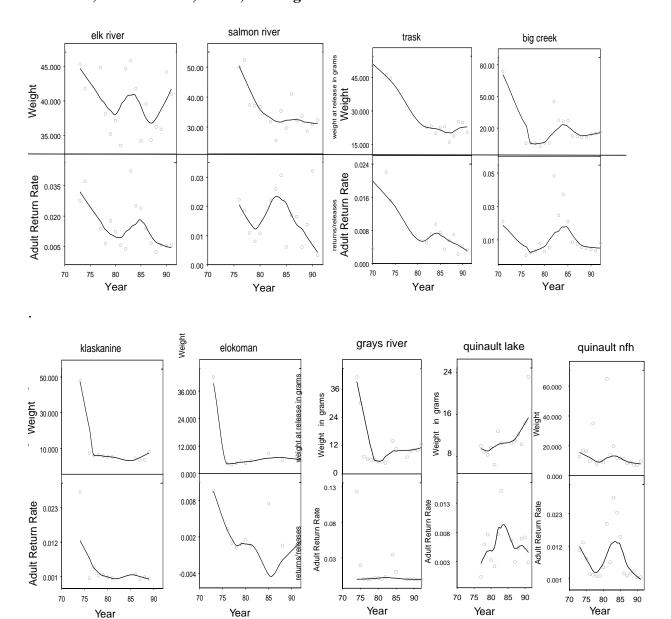


Figure D3: Return rates by release-month indices for combined (across hatchery) data. The release-month indices are weighted averages of release-month per brood-year, i.e., there is one release-month index for each brood-year. The indices are computed by taking the summation (over all batches in a brood-year, i.e., across hatcheries) of (batch) release-month multiplied by (batch) releases divided by total yearly (across batches) releases.

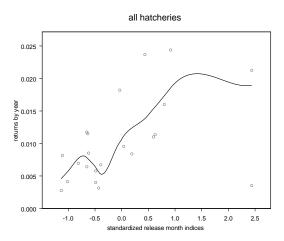


Table E1 contains the estimated regression coefficients for the nine models selected as both significant and best-fitting (Table 3.11). The column headings in Table E1 refer to the coefficients as they are numbered in model 3.1, below.

$$S_{1} = S_{0}^{e} S_{0}^{Wt + \beta_{2}Wt^{2} + \beta_{3}Cov + \beta_{4}Cov^{2}},$$

Table E1: Regression coefficient estimates for eq. 3.1 for significant best-fitting models (Table 3.11) relating ocean covariates to first ocean-year survival.

Ocean Covariate	Hatchery	$\hat{eta}_1$	$\hat{eta}_2$	$\hat{eta}_3$	$\hat{eta}_4$	
	Abernathy	-0.0067	0.0093	0.0617	0.0402	
	Big Creek	-0.249	0.0626	0.0501	-0.0333	
	Elk River	-0.0095	-0.0358	0.0858	-0.0072	
	Elokoman	-0.6482	0.215	0.0413	0.105	
April SST	Grays River	-0.2135	0.0766	0.1152	-0.0478	
	Klaskanine	0.0701	-0.0331	0.1429	-0.1828	
	Quin. NFH	-0.148	0.0355	0.0274	-0.0084	
	Quin. Lake	-0.056	0.0371	-0.0312	0.0113	
	Salm. River	0.0406	-0.0277	0.0884	-0.0183	
	Trask	-0.066	0.0178	0.0332	-0.0028	
	Abernathy	-0.0039	0.0116	0.0196	0.0109	
	Big Creek	-0.3038	0.0772	0.025	0.0094	
	Elk River	-0.0156	-0.0121	0.0561	-0.0246	
	Elokoman	-0.5271	0.1626	-0.0247	0.0213	
June SST	Grays River	-0.4721	0.1324	-0.0104	0.0824	
	Klaskanine	-0.0972	-0.0228	-0.0184	-0.0461	
	Quin. NFH	-0.1906	0.0512	0.0399	-6e-04	
	Quin. Lake	-0.1296	0.05	0.0952	-0.006	
	Trask	-0.0168	-0.0249	0.0327	-0.0144	

Table E1: Regression coefficient estimates for eq. 3.1 for significant best-fitting models (Table 3.11) relating ocean covariates to first ocean-year survival.

Ocean Covariate	Hatchery	$\hat{eta}_1$	$\hat{eta}_2$	$\hat{oldsymbol{eta}}_3$	$\hat{eta}_4$
	Abernathy2	0.0292	-0.0217	0.0648	-0.0339
	Big Creek	-0.2742	0.067	0.0021	-0.0243
	Elk River	-0.0111	-0.0678	0.0401	-0.0258
	Elokoman	-0.4916	0.1562	0.0709	0.0551
November	Grays River	-0.1022	-0.0312	0.1472	-0.02
SST	Klaskanine	-0.2149	0.0736	0.2731	-0.1885
	Quin. NFH	-0.1259	0.0285	0.0815	-0.0065
	Quin. Lake	-0.09	0.0502	-0.1475	0.0661
	Salm. River	0.0079	-0.0202	0.0639	-0.0078
	Trask	-0.0578	0.0183	0.043	0.016
	Abernathy	0.0103	-0.0082	0.0133	-0.01
	Big Creek	-0.2736	0.0723	0.0173	-0.0311
	Elk River	-0.0047	-0.1358	0.084	-0.0972
December	Elokoman	-0.4942	0.1452	0.0721	0.1069
SST	Grays River	-0.0164	-0.0278	0.2287	-0.086
	Quin. NFH	-0.0859	0.0119	0.0947	-0.0082
	Quin. Lake	-0.0651	0.0392	0.0447	-0.045
	Salm. River	-2e-04	-0.01	0.0531	-0.0051
	Trask	-0.038	-0.0321	0.0208	0.0421

Table E1: Regression coefficient estimates for eq. 3.1 for significant best-fitting models (Table 3.11) relating ocean covariates to first ocean-year survival.

Ocean Covariate	Hatchery	$\hat{eta}_1$	$\hat{eta}_2$	$\hat{eta}_3$	$\hat{eta}_4$	
	Abernathy	-0.1112	0.0684	0.0175	-0.1112	
	Big Creek	-0.3047	0.0772	0.0276	-0.0118	
	Elk River	-0.0663	-0.0252	0.0613	-0.0114	
December Upwelling	Elokoman	-0.4925	0.1425	0.0828	0.0445	
at 42°N	Grays River	-0.3879	0.0554	0.1968	0.0911	
	Quin. NFH	-0.1575	-0.0042	-0.0169	-0.0115	
	Quin. Lake	-0.2458	0.0683	0.0714	0.0818	
	Abernathy	-0.0861	0.0453	0.0141	-0.0051	
	Trask	-0.0524	-0.0123	0.0426	0.0073	
	Abernathy	-1e-04	0.0014	-0.0256	0.0073	
	Big Creek	-0.2902	0.0724	-0.0082	-0.0018	
	Elk River	-0.0725	0.0498	-0.0955	-0.0677	
January Upwelling	Elokoman	0.4983	-0.2272	-0.0638	-0.0873	
at 45°	Grays River	-0.5373	0.1454	0.0674	0.0053	
	Klaskanine	-0.2161	0.0114	0.0627	0.0232	
	Quin. NFH	-0.2081	0.0524	-0.0904	-0.06	
	Quin. Lake	-0.062	0.0318	-0.0836	-0.0552	
	Salm. River	0.0146	-0.0242	-0.0187	0.0231	
	Trask	-0.0329	-0.0107	-0.0443	-0.019	

Table E1: Regression coefficient estimates for eq. 3.1 for significant best-fitting models (Table 3.11) relating ocean covariates to first ocean-year survival.

Ocean Covariate	Hatchery	$\hat{eta}_1$	$\hat{eta}_2$	$\hat{oldsymbol{eta}}_3$	$\hat{eta}_4$	
	Abernathy	-0.0067	-0.0084	-0.0151	-0.0445	
	Big Creek	-0.26	0.0646	-0.0135	-0.0369	
	Elk River	-0.061	-0.052	-0.1236	0.0365	
July Upwelling	Elokoman	-0.4079	0.0894	-0.1337	0.0717	
at $48^{\circ}$	Grays River	-0.2994	0.0231	-0.1333	-0.0509	
	Klaskanine	-0.158	-0.0044	-6e-04	0.0086	
	Quin. NFH	-0.1651	0.0372	-0.0272	-0.0382	
	Quin. Lake	-0.0562	0.0282	0.0087	-0.0557	
	Salm. River	0.0311	-0.0494	0.0718	-0.0758	
	Trask	-0.0445	-0.0195	0.0068	-0.0469	
	Abernathy	-0.0763	0.0195	0.0968	-0.0907	
	Big Creek	-0.2587	0.062	0.0432	0.0058	
	Elk River	-0.0664	-4e-04	0.0125	-0.0443	
December Upwelling	Elokoman	-0.0079	-0.0376	0.0323	-0.0422	
at 48°	Grays River	-0.3899	0.0347	0.2292	0.0367	
	Klaskanine	0.1891	-0.1434	0.0398	-0.1194	
	Quin. NFH	-0.2133	0.0528	0.0572	-0.011	
	Quin. Lake	-0.0687	0.0396	0.0158	0.0035	
	Salm. River	0.1318	-0.1183	0.0921	0.0771	
	Trask	-0.042	-0.022	0.0321	0.0098	

Table E1: Regression coefficient estimates for eq. 3.1 for significant best-fitting models (Table 3.11) relating ocean covariates to first ocean-year survival.

Ocean Covariate	Hatchery	$\hat{eta}_1$	$\hat{eta}_2$	$\hat{eta}_3$	$\hat{eta}_4$
	Abernathy	0.0018	-0.0059	0.2796	-0.2105
	Big Creek	-0.2673	0.0681	0.0393	0.0248
	Elk River	-0.0762	-0.0645	0.0548	0.123
Northward Upwelling	Elokoman	-0.5215	0.147	0.0691	0.0451
Extent in June (JNUE)	Grays River	-0.4628	0.1369	0.2007	0.0362
June (JIVOL)	Klaskanine	-0.4567	0.0978	-0.0201	-0.0651
	Quin. NFH	-0.1981	0.0431	0.0249	0.0539
	Quin. Lake	-0.0814	0.0297	0.048	0.042
	Salm. River	0.0284	-0.0362	0.0158	-0.0148
	Trask	-0.0416	-0.0027	-0.0285	-0.003

**Table F1: Correlations between SST-months.** 

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Jan	1.00											
Feb	0.62	1.0										
Mr	0.58	0.9	1.0									
Apr	0.49	0.5	0.6	1.0								
May	0.49	0.3	0.3	0.5	1.00							
Jun	0.33	0.4	0.5	0.6	0.28	1.0						
Jul	0.06	-0.2	0.0	0.4	0.39	0.5	1.00					
Aug	0.18	-0.1	-0.1	0.4	0.20	0.3	0.46	1.0				
Sep	0.14	-0.2	-0.1	0.2	-0.16	0.2	0.30	0.6	1.00			
Oct	0.49	0.1	0.3	0.4	0.17	0.5	0.33	0.3	0.68	1.0		
Nov	0.52	0.3	0.4	0.6	0.40	0.2	0.31	0.3	0.47	0.7	1.00	
Dec	0.45	0.4	0.5	0.6	0.29	0.2	0.24	0.2	0.43	0.6	0.88	1.0

Table F2: Correlations between Upwelling-Months at  $42\,^{\circ}\,N$  .

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Jan	1.00											
Feb	0.44	1.00										
Mar	0.41	0.54	1.00									
Apr	-0.08	0.06	0.30	1.00								
May	0.27	-0.07	0.19	0.11	1.00							
Jun	0.49	0.05	0.36	0.36	0.37	1.00						
Jul	-0.04	0.07	0.45	0.23	-0.17	0.06	1.00					
Aug	0.08	0.05	0.23	0.31	0.07	0.04	0.24	1.00				
Sep	0.31	-0.11	-0.20	-0.09	0.05	0.32	-0.04	-0.04	1.00			
Oct	0.13	0.13	0.04	0.03	0.17	0.30	0.08	0.04	0.12	1.00		
Nov	0.18	0.58	0.45	0.05	0.05	0.07	0.21	0.17	0.06	0.26	1.00	
Dec	0.05	0.03	-0.31	-0.17	-0.05	-0.02	-0.05	-0.15	0.45	0.34	0.10	1.00

Table F3: Correlation matrices between Bakun upwelling indices at 42, 45, 48°N latitude, by month.

month	correlation matrix between upwelling indices at 42,45, and $48^{0}$ N latitude
jan	42 45 48
	42 1.0000000 0.9526227 0.8685203
	45 0.9526227 1.0000000 0.9530837
	48 0.8685203 0.9530837 1.0000000
feb	42 45 48
	42 1.0000000 0.9316666 0.8643289
	45 0.9316666 1.0000000 0.9198863
	48 0.8643289 0.9198863 1.0000000
mar	42 45 48
	42 1.0000000 0.9107037 0.7705974
	45 0.9107037 1.0000000 0.9302242
	48 0.7705974 0.9302242 1.0000000
apr	42 45 48
	42 1.0000000 0.8238049 0.7126166
	45 0.8238049 1.0000000 0.9503914
	48 0.7126166 0.9503914 1.0000000
may	42 45 48
	42 1.0000000 0.8618583 0.5958931
	45 0.8618583 1.0000000 0.8586020
	48 0.5958931 0.8586020 1.0000000

Table F3: Correlation matrices between Bakun upwelling indices at 42, 45, 48°N latitude, by month.

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month	correlation matrix between upwelling indices at 42,45, and $48^{0}$ N latitude
jun	42 45 48
	42 1.0000000 0.7910686 0.3681918
	45 0.7910686 1.0000000 0.8091793
	48 0.3681918 0.8091793 1.0000000
jul	42 45 48
	42 1.0000000 0.7414269 0.4141928
	45 0.7414269 1.0000000 0.8175704
	48 0.4141928 0.8175704 1.0000000
aug	42 45 48
	42 1.0000000 0.8475586 0.5001935
	45 0.8475586 1.0000000 0.8445200
	48 0.5001935 0.8445200 1.0000000
sep	42 45 48
r	42 1.0000000 0.7823081 0.5261006
	45 0.7823081 1.0000000 0.7980622
	48 0.5261006 0.7980622 1.0000000
oct	42 45 48
	42 1.0000000 0.8134276 0.6695958
	45 0.8134276 1.0000000 0.9022540
	48 0.6695958 0.9022540 1.0000000
nov	42 45 48
	42 1.0000000 0.9015203 0.7432397
	45 0.9015203 1.0000000 0.9140473
	48 0.7432397 0.9140473 1.0000000

Table F3: Correlation matrices between Bakun upwelling indices at 42, 45, 48°N latitude, by month.

month	correlation matrix between upwelling indices at 42,45, and $48^{0}$ N latitude
dec	42 45 48 42 1.0000000 0.9360572 0.7352233 45 0.9360572 1.0000000 0.8832412 48 0.7352233 0.8832412 1.0000000

Table F4: Correlations between SST-Months and Upwelling Months at  $42^{\circ}\,N$  latitude.

	JanU	FebU	MarU	AprU	MayU	JunU	JulU	AugU	SepU	OctU	NovU	DecU
JanT	-0.6	-0.45	-0.39	-0.12	-0.25	-0.58	-0.02	-0.09	-0.19	-0.53	-0.47	0.11
FebT	-0.7	-0.54	-0.21	0.14	-0.05	-0.29	0.31	0.27	0.15	-0.11	-0.29	0.06
MarT	-0.7	-0.65	-0.20	0.10	-0.24	-0.32	0.22	0.26	0.05	-0.14	-0.38	-0.12
AprT	-0.5	-0.51	-0.61	-0.19	-0.29	-0.48	-0.07	0.09	0.13	-0.12	-0.29	0.06
MayT	-0.2	-0.36	-0.35	-0.11	-0.23	-0.39	-0.18	0.27	-0.2	-0.22	-0.36	0.03
JunT	-0.6	-0.30	-0.41	-0.44	-0.36	-0.48	0.13	-0.07	-0.1	0.14	0.13	0.15
JulT	-0.1	-0.23	-0.50	-0.51	-0.23	-0.34	-0.53	-0.12	-0.08	-0.01	0.08	0.08
AugT	0.1	0.03	-0.51	-0.50	-0.27	-0.37	-0.22	-0.57	0.09	-0.10	-0.15	0.27
SepT	0.1	0.08	-0.15	-0.46	-0.07	-0.12	-0.14	-0.51	-0.23	-0.04	-0.06	0.03
OctT	-0.3	-0.23	-0.20	-0.51	-0.39	-0.26	0.06	-0.19	-0.29	-0.25	-0.21	-0.09
NovT	-0.2	-0.40	-0.20	-0.43	-0.10	-0.21	-0.14	0.07	-0.03	-0.35	-0.42	-0.09
DecT	-0.3	-0.33	-0.17	-0.32	0.04	-0.20	-0.19	0.13	-0.03	-0.27	-0.39	-0.17

Table F5: Correlations between Upwelling months at  $42\,^{\circ}\,N$  and climate indices.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
cum45	0.36	0.14	0.64	0.48	0.50	0.36	0.18	0.39	0.01	-0.03	0.34	-0.19
cum48	0.09	0.01	0.28	0.13	0.24	-0.12	-0.23	0.09	-0.33	-0.51	0.00	-0.42
npi	0.76	0.54	0.34	0.10	0.33	0.31	-0.15	-0.01	0.23	0.26	0.40	0.07
nue	0.33	0.16	0.14	-0.24	0.57	0.23	-0.06	-0.15	0.08	0.41	0.58	0.15
pni	-0.46	-0.21	-0.08	-0.31	-0.28	-0.34	0.25	0.07	-0.27	-0.41	-0.13	-0.25

Table F6: Corrlations between SST and Climate Indices.

	cum45	cum48	npi	nue	pni
janT	-0.3	0.21	-0.7	-0.48	0.47
febT	-0.1	-0.07	-0.8	-0.33	0.46
marT	-0.1	-0.02	-0.8	-0.36	0.41
aprT	-0.4	-0.19	-0.4	-0.18	0.28
mayT	-0.2	0.03	-0.3	-0.44	0.28
junT	-0.5	-0.40	-0.5	0.01	0.48
julT	-0.2	0.03	0.0	0.15	0.02
augT	-0.4	-0.11	0.0	-0.09	0.17
sepT	-0.2	0.05	0.0	0.09	0.06
octT	-0.4	-0.02	-0.5	-0.28	0.60
novT	-0.2	0.08	-0.4	-0.23	0.39
decT	-0.1	0.20	-0.4	-0.13	0.40

Table F7: Correlations between climate indices.

	cu45	cu48	npi	nue	pni
cu45	1.00				
cu48	0.64	1.00			
npi	0.35	0.07	1.00		
nue	0.31	0.05	0.51	1.00	
pni	-0.21	0.09	-0.62	-0.34	1.00

Figure G1: Fitted curves (using model 3.1) of first ocean-year survival against covariates (January-April SST), after adjustment for weight-at-release.

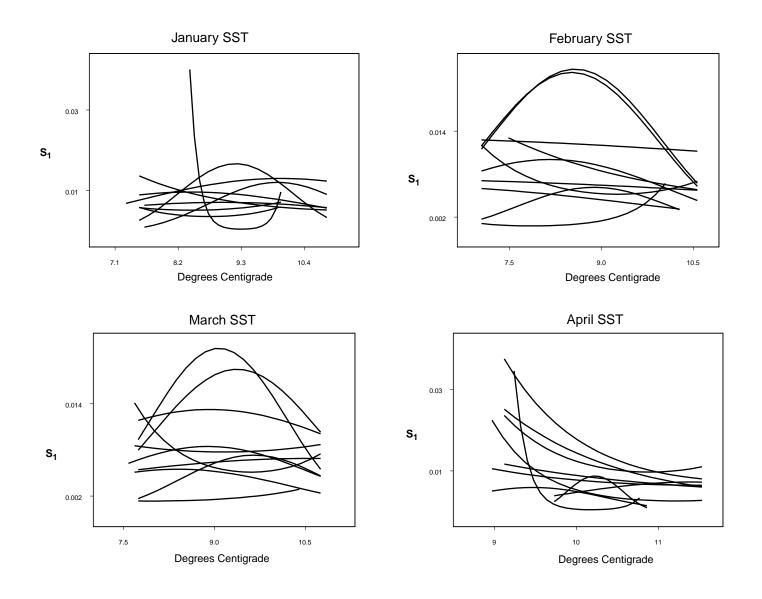


Figure G2: Fitted curves (using model 3.1) of first ocean-year survival against covariates (May-August SST), after adjustment for weight-at-release.

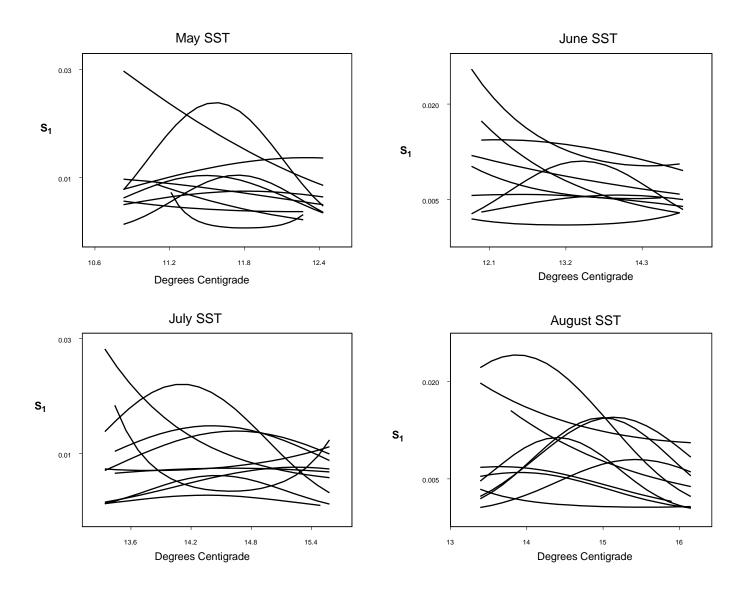


Figure G3: Fitted curves (using model 3.1) of first ocean-year survival against covariates (September SST), after adjustment for weight-at-release.

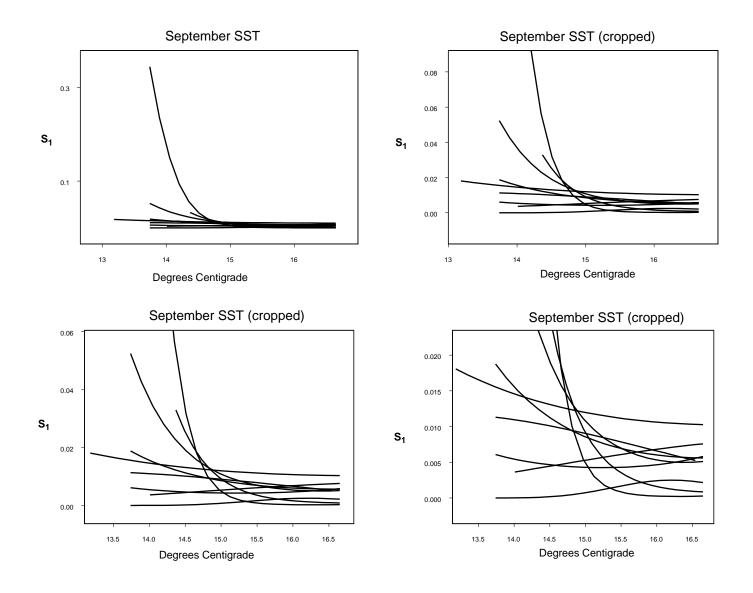


Figure G4: Fitted curves (using model 3.1) of first ocean-year survival against covariates (October-December SST), after adjustment for weight-at-release.

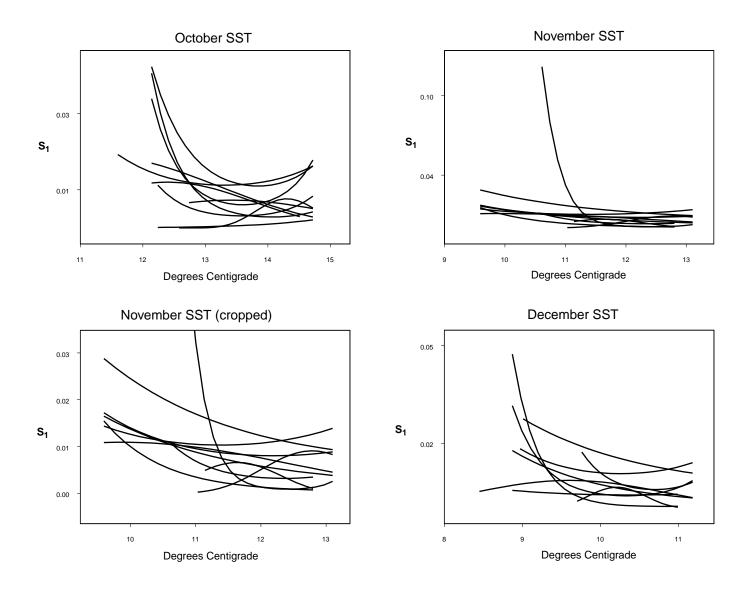


Figure G5: Fitted curves (using model 3.1) of first ocean-year survival against covariates (January-April Upwelling at 42°N latitude), after adjustment for weight-at-release.

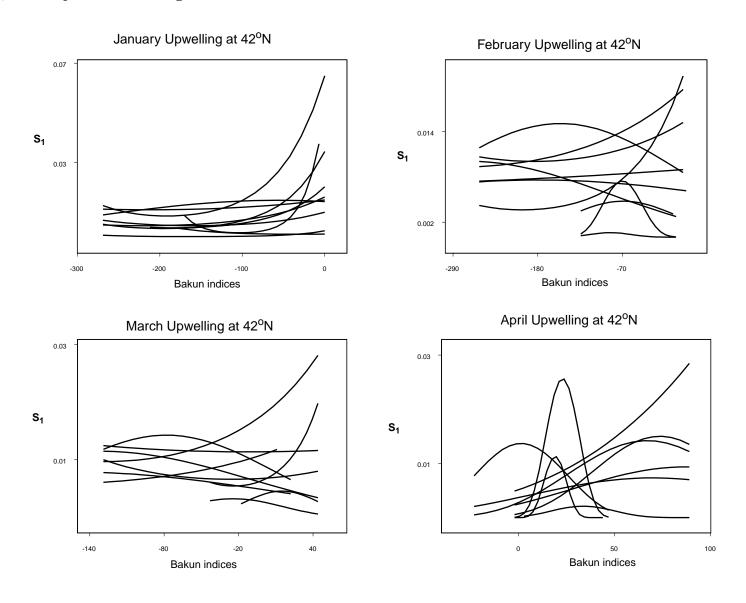


Figure G6: Fitted curves (using model 3.1) of first ocean-year survival against covariates (May-August Upwelling at 42<sup>o</sup>N latitude), after adjustment for weight-at-release.

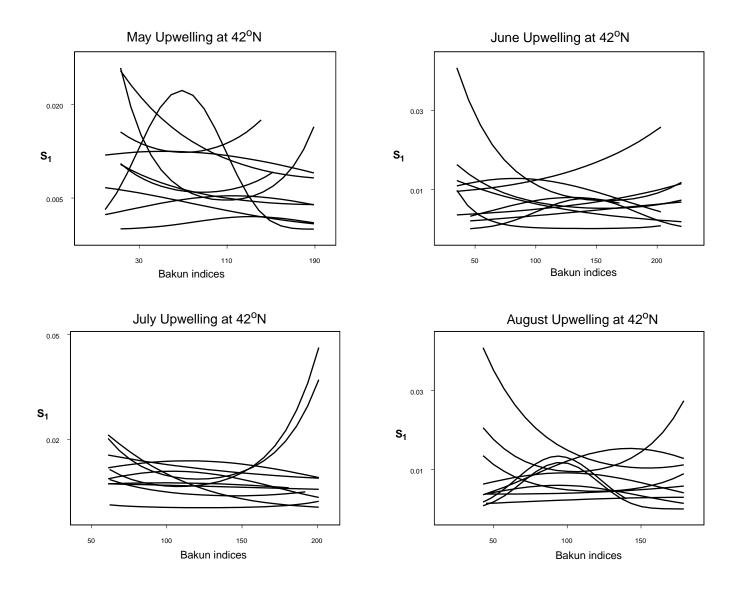


Figure G7: Fitted curves (using model 3.1) of first ocean-year survival against covariates (September-December Upwelling at 42°N latitude), after adjustment for weight-at-release.

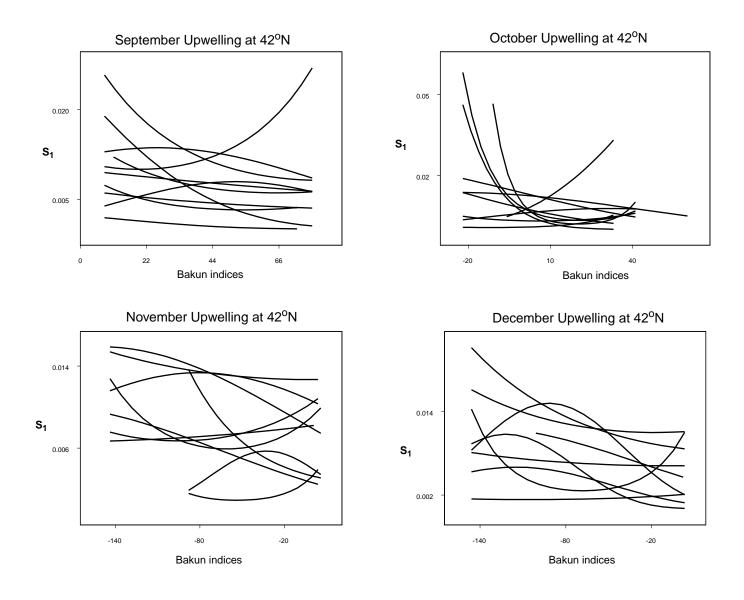


Figure G8: Fitted curves (using model 3.1) of first ocean-year survival against covariates (January-April Upwelling at 45°N latitude), after adjustment for weight-at-release.

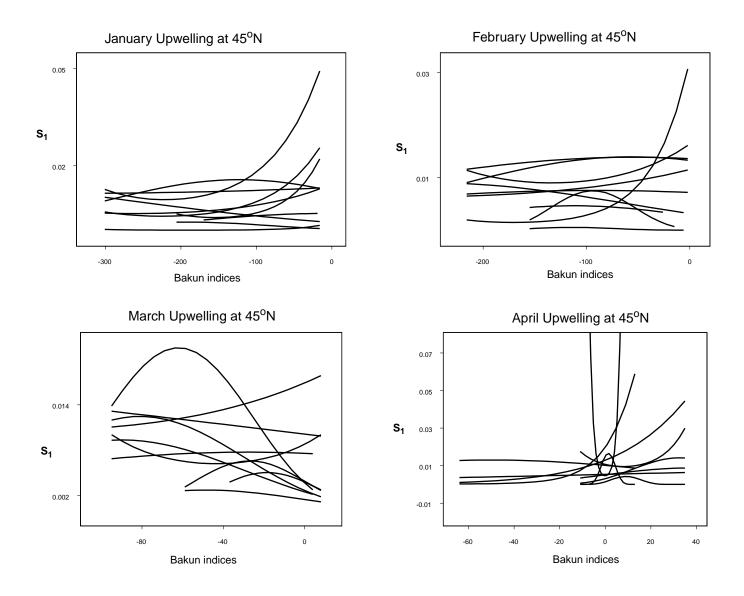


Figure G9: Fitted curves (using model 3.1) of first ocean-year survival against covariates (May-August Upwelling at 45°N latitude), after adjustment for weight-at-release.

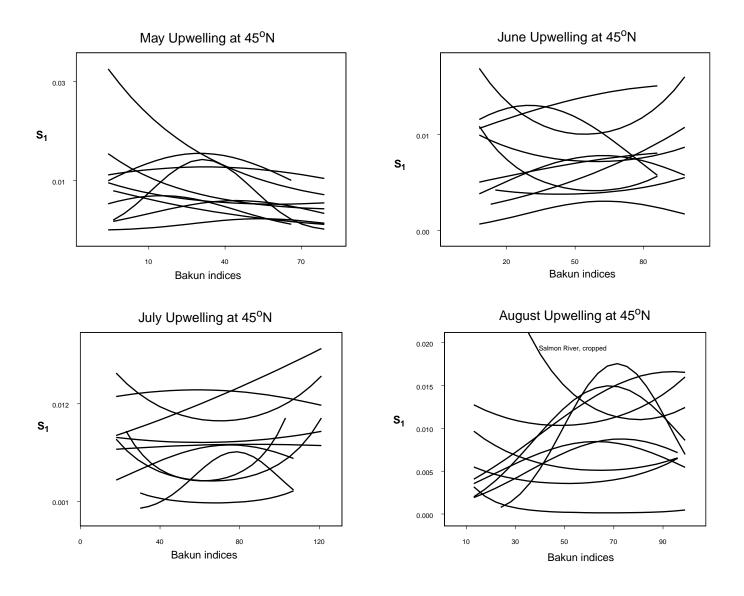


Figure G10: Fitted curves (using model 3.1) of first ocean-year survival against covariates (September-December Upwelling at 45°N latitude), after adjustment for weight-at-release.

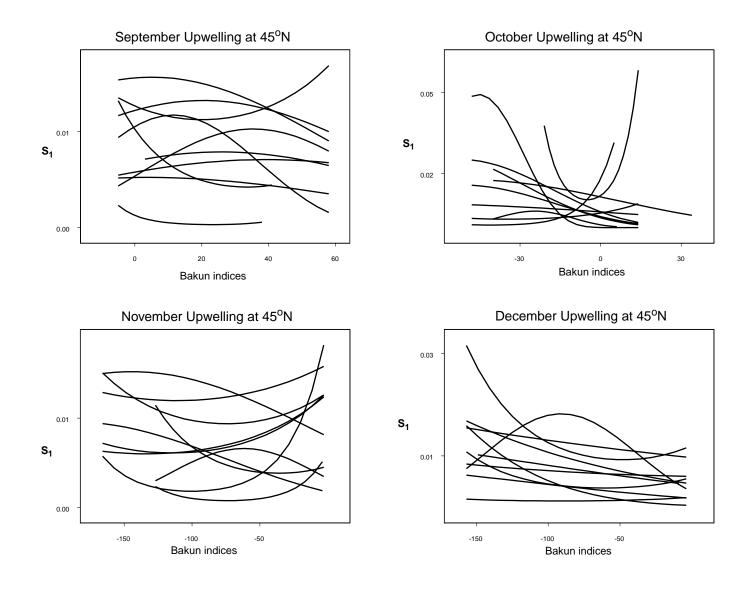


Figure G11: Fitted curves (using model 3.1) of first ocean-year survival against covariates (January-April Upwelling at 48°N latitude), after adjustment for weight-at-release.

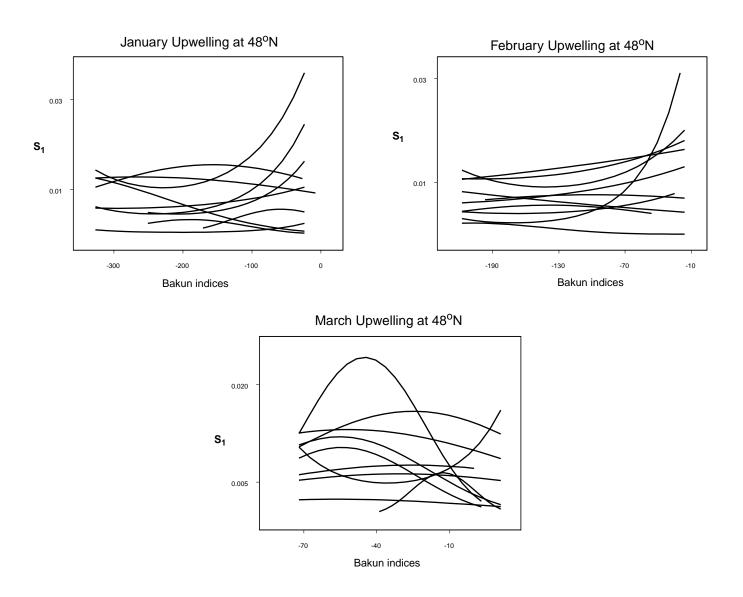


Figure G12: Fitted curves (using model 3.1) of first ocean-year survival against covariates (April-June Upwelling at 48°N latitude), after adjustment for weight-at-release.

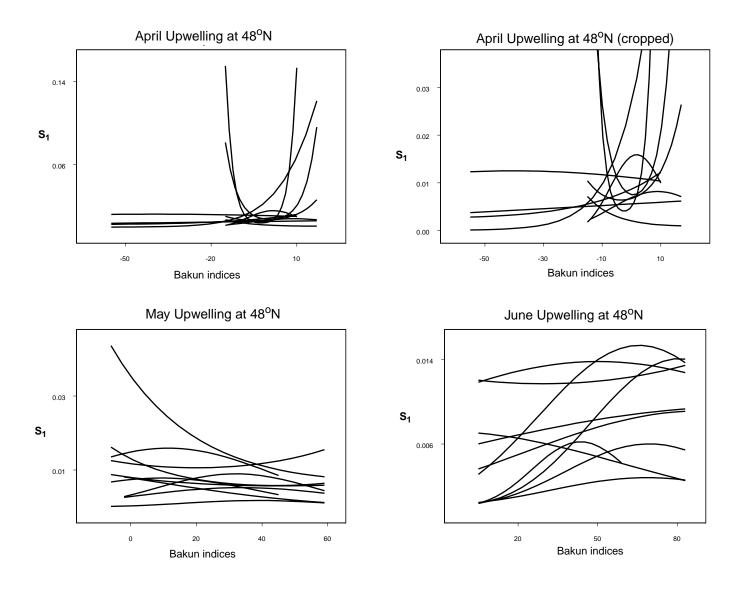


Figure G13: Fitted curves (using model 3.1) of first ocean-year survival against covariates (July-October Upwelling at 48°N latitude), after adjustment for weight-at-release.

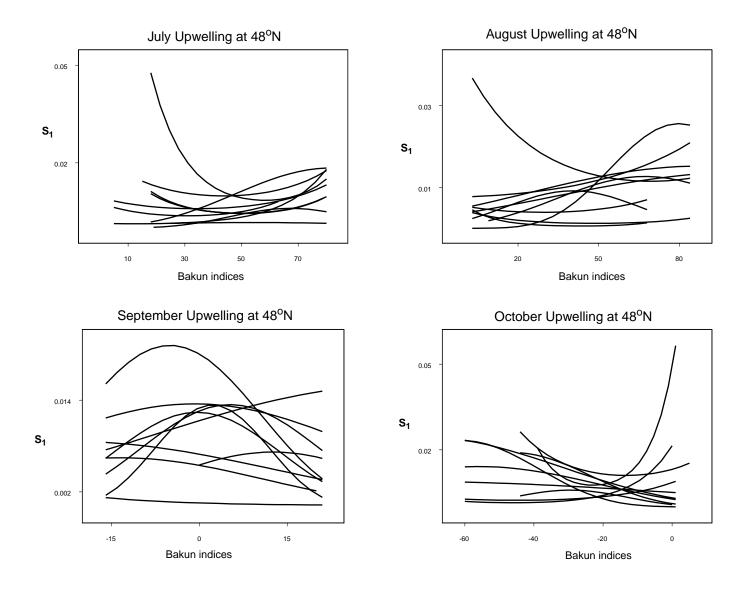
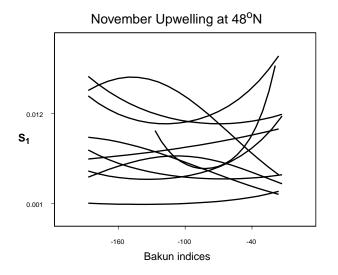


Figure G14: Fitted curves (using model 3.1) of first ocean-year survival against covariates (November-December Upwelling at 48°N latitude), after adjustment for weight-at-release.



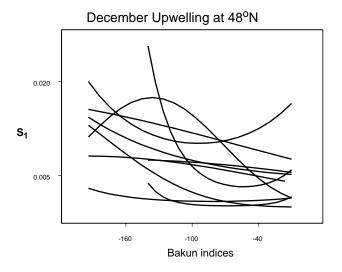
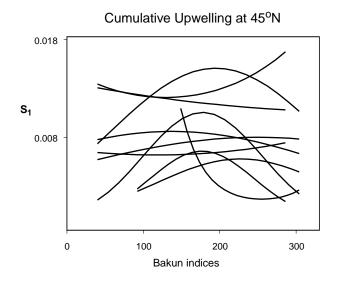


Figure G15: Fitted curves (using model 3.1) of first ocean-year survival against covariates (cumulative May-September upwelling at  $45^{\circ}$  and  $48^{\circ}$ N latitude), after adjustment for weight-at-release.



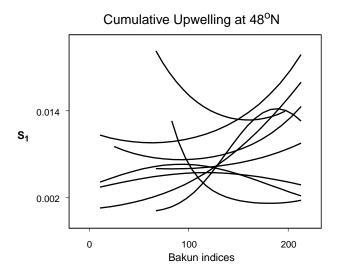
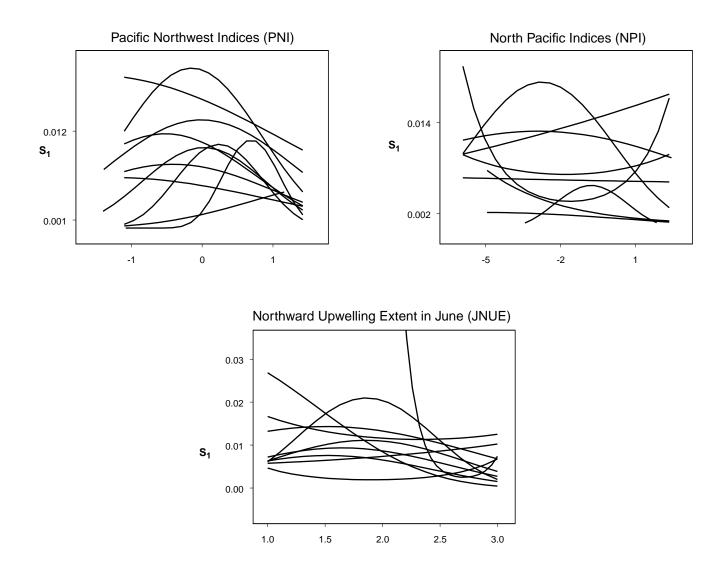


Figure G16: Fitted curves (using model 3.1) of first ocean-year survival against covariates (Pacific Northwest Indices, PNI; North Pacific Indices, NPI; Northward Extent of Upwelling in June, JNUE) after adjustment for weight-at-release.



## Ocean Covariates and Survival: SST, Upwelling, Climate

Figure H1: Loess-fitted by-hatchery plots of return rates against sea surface temperurature during Januray, February, March and April. Return rates were computed per cohort (fish released in a brood year), and temperatures were measured during the release year (brood year plus one).

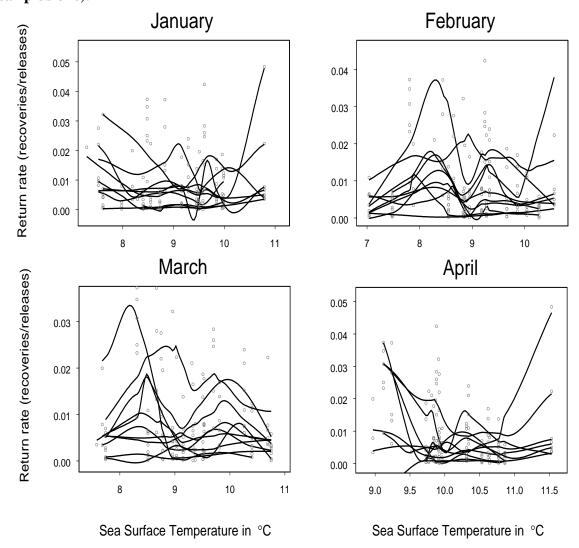


Figure H2: Loess-fitted by-hatchery plots of return rates against sea surface temperurature during May, June, July and August. Return rates were computed per cohort (fish released in a brood year), and temperatures were measured during the release year (brood year plus one).

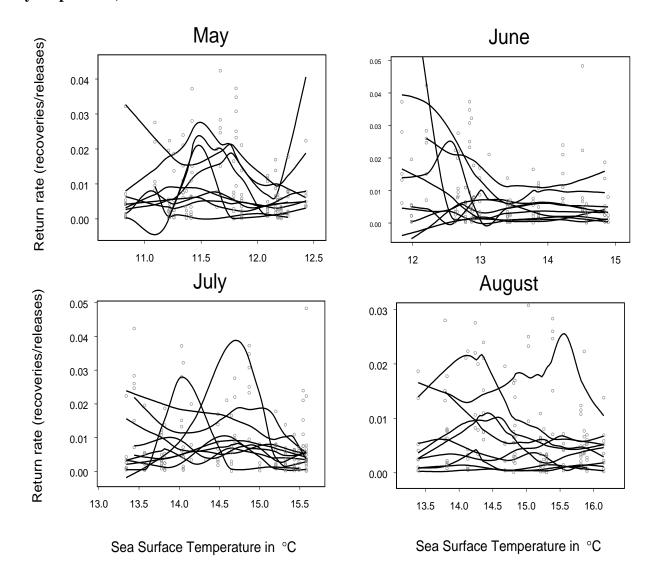


Figure H3: Loess-fitted by-hatchery plots of return rates against sea surface temperurature during September, October, November and December. Return rates were computed per cohort (fish released in a brood year), and temperatures were measured during the release year (brood year plus one).

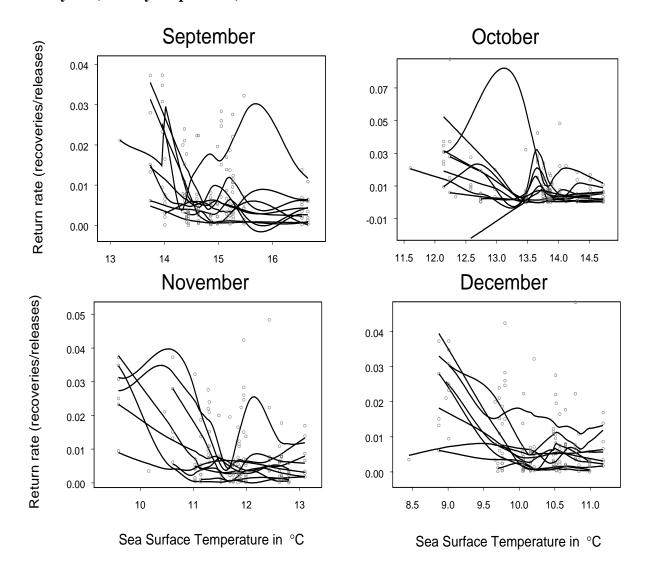
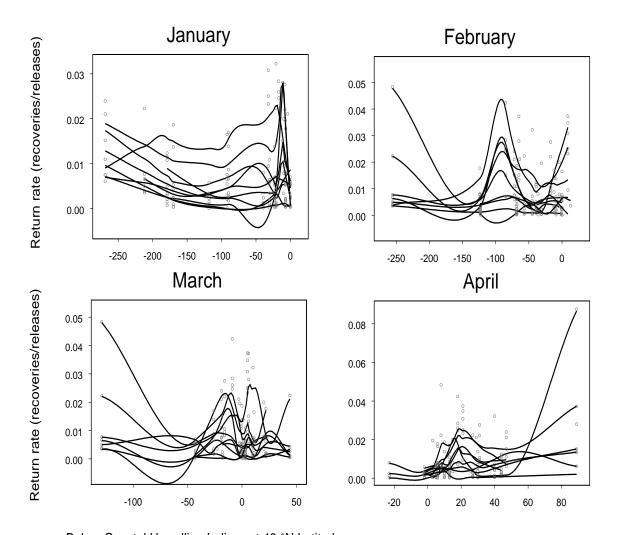
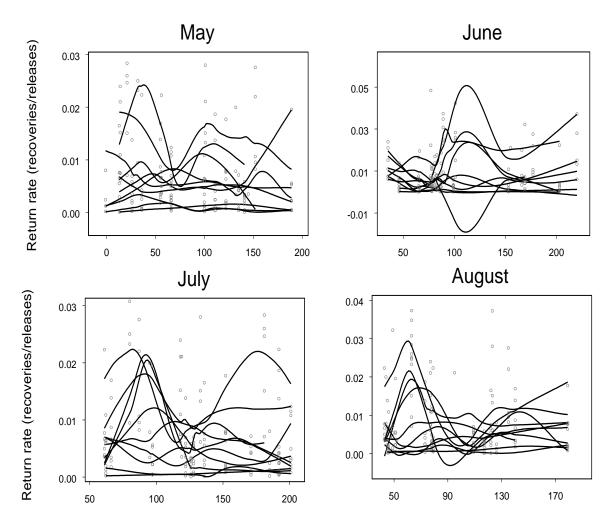


Figure H4: Loess-fitted by-hatchery plots of return rates against Bakun coastal upwelling indices at 42°N latitude during January, February, March and April. Return rates were computed per cohort (fish released in a brood year), and upwelling indices were measured during the release year (brood year plus one).



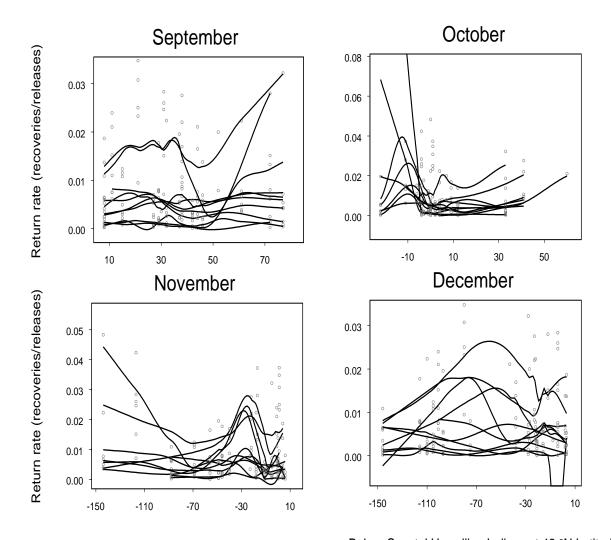
Bakun Coastal Upwelling Indices at 42 °N Latitude Bakun Coastal Upwelling Indices at 42 °N Latitude

Figure H5: Loess-fitted by-hatchery plots of return rates against Bakun coastal upwelling indices at 42°N latitude during May, June, July and August. Return rates are computed per cohort (fish released in a brood year), and upwelling indices were measured during the release year (brood year plus one).



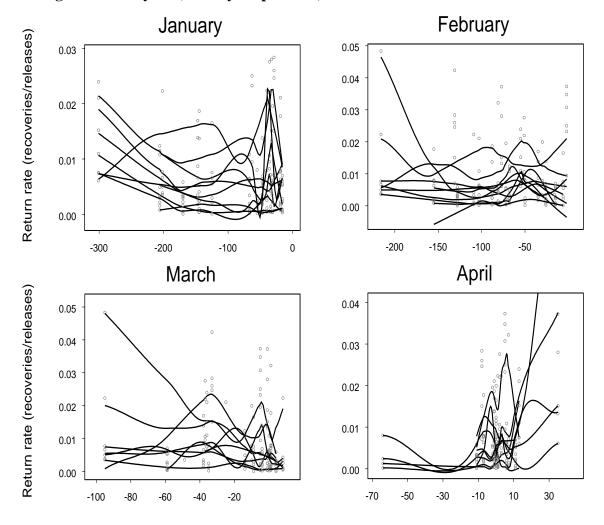
Bakun Coastal Upwelling Indices at 42 °N Latitude Bakun Coastal Upwelling Indices at 42 °N Latitude

Figure H6: Loess-fitted, by-hatchery plots of return rates against Bakun coastal upwelling indices at 42°N latitude during September, October, November, December. Return rates were computed per cohort (fish released in a brood year), and upwelling indices were measured during the release year (brood year plus one).



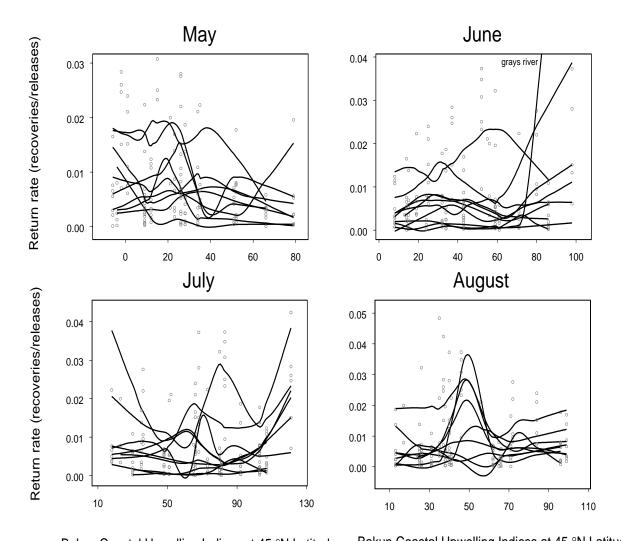
Bakun Coastal Upwelling Indices at 42 °N Latitude Bakun Coastal Upwelling Indices at 42 °N Latitude

Figure H7: Loess-fitted by-hatchery plots of return rates against Bakun coastal upwelling indices at 45°N latitude during January, February, March and April. Return rates were computed per cohort (fish released in a brood year), and upwelling indices were measured during the release year (brood year plus one).



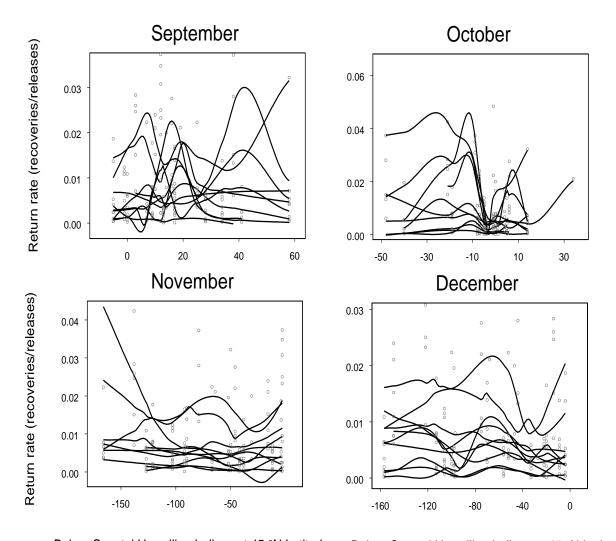
Bakun Coastal Upwelling Indices at 45 °N Latitude Bakun Coastal Upwelling Indices at 45 °N Latitude

Figure H8: Loess-fitted by-hatchery plots of return rates against Bakun coastal upwelling indices at 45°N latitude during May, June, July and August. Return rates were computed per cohort (fish released in a brood year), and upwelling indices were measured during the release year (brood year plus one).



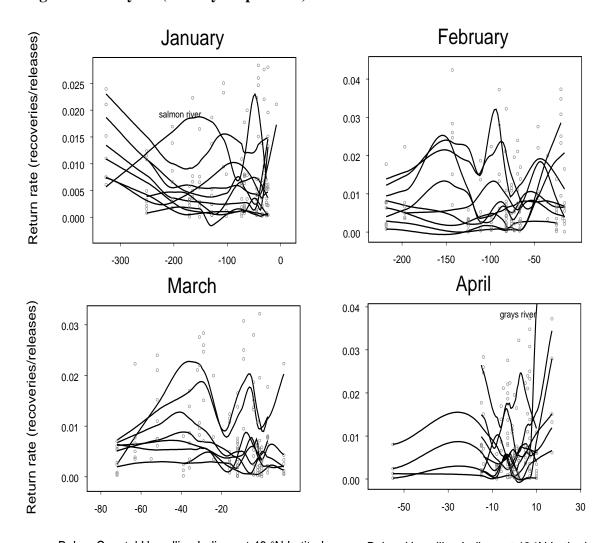
Bakun Coastal Upwelling Indices at 45 °N Latitude Bakun Coastal Upwelling Indices at 45 °N Latitude

Figure H9: Loess-fitted by-hatchery plots of return rates against Bakun coastal upwelling indices at 45°N latitude during September, October, November, and December. Return rates were computed per cohort (fish released in a brood year), and upwelling indices were measured during the release year (brood year plus one).



Bakun Coastal Upwelling Indices at 45 °N Latitude Bakun Coastal Upwelling Indices at 45 °N Latitude

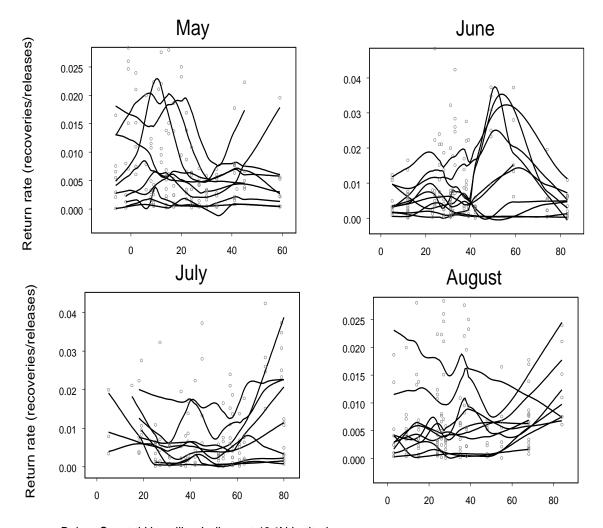
Figure H10: Loess-fitted by-hatchery plots of return rates against Bakun coastal upwelling indices at 48°N latitude during January, February, March and April. Return rates were computed per cohort (fish released in a brood year), and upwelling indices were measured during the release year (brood year plus one).



Bakun Coastal Upwelling Indices at 48 °N Latitude

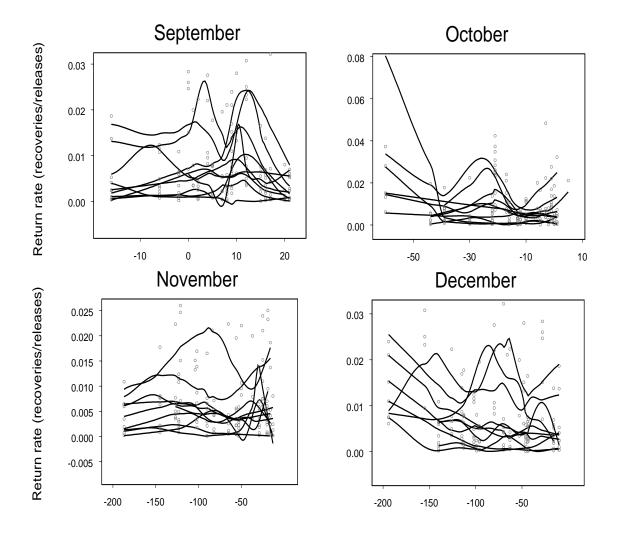
Bakun Upwelling Indices at 48 °N Latitude

Figure H11: Loess-fitted by-hatchery plots of return rates against Bakun coastal upwelling indices at 48°N latitude during May, June, July and August. Return rates were computed per cohort (fish released in a brood year), and upwelling indices were measured during the release year (brood year plus one).



Bakun Coastal Upwelling Indices at 48 °N Latitude Bakun Coastal Upwelling Indices at 48 °N Latitude

Figure H12: Loess-fitted by-hatchery plots of return rates against Bakun coastal upwelling indices at 48°N latitude during September, October, November, and December. Return rates were computed per cohort (fish released in a brood year), and upwelling indices were measured during the release year (brood year plus one).



Bakun Coastal Upwelling Indices at 48 °N Latitude Bakun Coastal Upwelling Indices at 48 °N Latitude

Figure H13: Loess-fitted by-hatchery plots of return rates against annually measured climate indices. Return rates were computed per cohort (fish released in a brood year), and indices were measured during the release year (brood year plus one).

